PB80-185267

Crabs (Arthropoda: Crustacea: Decapoda: Brachyura)

(U.S.) Environmental Research Lab.
Gulf Breeze, FL

1979

U.S. Department of Commerce
National Technical Information Service
NTIS.

TECHNICAL REPORT DATA

(Please read Instructions on the reverse before completing)

1. REPORT NO. EPA-600/J-79-082	2. JOURNAL ARTICLE
3. RECIPIENT	PB80-185267
4. TITLE AND SUBTITLE: CRABS (ARTHROPODA: CRUSTACEA: DECAPODA: BRACHYURA)	5. REPORT DATE
	6. PERFORMING ORGANIZATION CODE
7. AUTHOR(S): Austin B. Williams and Thomas W. Duke *	8. PERFORMING ORGANIZATION REPORT NO.
9. PERFORMING ORGANIZATION NAME AND ADDRESS: SAME AS BOX 12	10. PROGRAM ELEMENT NO. 1EA615
	11. CONTRACT/GRANT NO.
12. SPONSORING AGENCY NAME AND ADDRESS: *Environmental Research Laboratory, Office of Research and Development, U.S. Environmental Protection Agency, Gulf Breeze, Florida 32561	13. TYPE OF REPORT AND PERIOD COVERED: FINAL
	14. SPONSORING AGENCY CODE: EPA/600/04

15. SUPPLEMENTARY NOTES

Reference: In: Pollution Ecology of Estuarine Invertebrates, pp. 171-233. Academic Press, New York, 1979.

16. ABSTRACT

The effects of a few major pollutants on crabs are described. Because of their sensitivity to many forms of man-made pollution, crabs can often be used to predict adverse influences on the environment and to evaluate their effects. Crabs are viewed as having unaltered or "normal" life histories and ecology or altered life patterns possibly influenced by pollution in changing environments. The authors discuss these two categories and present the "normal" patterns as a set of specific vignettes that form a foundation for discussion of the observed effects of pollutants on four crab species.

REPRODUCED BY
NATIONAL TECHNICAL
INFORMATION SERVICE
U.S. DEPARTMENT OF COMMERCE
SPRINGFIELD, VA. 22161

17. KEY WORDS AND DOCUMENT ANALYSIS

a. DESCRIPTORS	b. IDENTIFIERS/OPEN ENDED TERMS	c. COSATI Field/Group
Crustacea Aquatic Life Aquatic Habitats Pollution Ecology Pesticides Systematics	Pollution studies Estuarine brachyuran crabs Thermal stress Chlorinated hydrocarbons Insect growth regulators	06/F 06/T 06/S 06/F

18. DISTRIBUTION STATEMENT: Unlimited	19. SECURITY CLASS *(This Report)*: Unclassified	21. NO. OF PAGES
	20. SECURITY CLASS *(This page)*: Unclassified	22. PRICE

EPA-600/J-79-082
JOURNAL ARTICLE

CHAPTER 6

Crabs (Arthropoda: Crustacea: Decapoda: Brachyura)

AUSTIN B. WILLIAMS and THOMAS W. DUKE

I. Introduction 171
II. Taxonomy 172
III. Normal Life History-Ecology 174
A. Family Cancridae 174
B. Family Portunidae 176
C. Family Xanthidae 180
D. Family Grapsidae 185
E. Family Ocypodidae 188
IV. Pollution Ecology 193
A. Pesticides 193
B. Thermal Effects 203
C. Oil 210
D. Metals 212
E. Radionuclides 219
V. Conclusions 221
References 222

I. Introduction

Biological research on estuarine brachyuran crabs has centered on a few species found literally at the doorstep of marine laboratories. The abundance and

1979 by Academic Press, Inc

2

accessibility of these species for field study, coupled with their capability for successful manipulation in laboratory experiments, have helped to promote a good understanding of their systematic position, physiology, ecology, and reaction to environmental alteration. A few species having significant value in fisheries have been similarly studied with somewhat greater effort, but the combined list is short, and if further limited to the subject matter covered in this book, it becomes even shorter. Acknowledging this, we have chosen to limit discussion a step further by confining this chapter primarily to species occurring in North America, feeling that effects of pollution on crabs in estuaries can be amply demonstrated by those species, but including data for other species when it seems productive to do so.

Crabs can be viewed as having unaltered or "normal" life histories and ecology as well as altered life patterns possibly brought on by pollution in changing environments. Because we deal in detail with only a few species, we have chosen to discuss these two fields of interest differently, presenting what is viewed as "normal" as a set of specific vignettes which form a foundation for discussion of the observed effects of pollution. Included in the "normal" set are four species not specifically discussed in the section on observed effects of pollution but which are intimately associated with communities reported here and treated in results of pollution studies elsewhere.

II. Taxonomy

The classification of the infraorder Brachyura long accepted by American scientists is that elaborated by Rathbun (1918, 1930) in her set of monographs on crabs of the Western Hemisphere. Gradually that system is being modified to accommodate new findings from the fossil record, adult morphology of living species, and larval development, as well as physiological, biochemical, and ecological studies.

Among the Brachyura, the most primitive groups generally have not successfully invaded estuaries in North America. None of the dromiaceans or the oxystomian box crabs and their relatives (Oxystomata) are found in any but the most seaward reaches of high-salinity estuaries, if present at all. Moreover, the great spider crab section (Oxyrhyncha) is essentially a euhaline marine group, only a few of its members being regularly encountered in lower reaches of estuaries, and none have figured in pollution studies. But members of the section Cancridea, *Cancer*, are found to some extent in estuaries, while those of the more highly specialized section Brachyrhyncha, including certain swimming crabs, mud crabs, square-backed crabs, and fiddlers, make up the conspicuously successful estuarine group. Among these are species of concern in pollution studies (Table I).

TABLE I

TAXONOMIC POSITION AND HABITAT OF DECAPOD CRUSTACEAN SPECIES, INFRAORDER BRACHYURA, OF CONCERN IN ESTUARINE POLLUTION STUDIES

Taxon	Habitat
Infraorder Brachyura	
Section Cancridea	
Family Cancridae	
Cancer irroratus Say, Rock crab	Temperate-polyhaline
Cancer magister Dana, Dungeness crab	
Section Brachyrhyncha	
Superfamily Portunoidea	
Family Portunidae, "Swimming" crabs	
Subfamily Portuninae	
Callinectes sapidus Rathburn, Blue crab	Temperate-tropical-euryhaline
Carcinus maenas (Linnaeus), Green or shore crab	Temperate-polyhaline
Superfamily Xanthoidea	
Family Xanthidae	
Subfamily Xanthinae, "Mud" crabs	
Cataleptodius (=*Leptodius*) *floridanus* (Gibbes)	Tropical-polyhaline
Eurypanopeus depressus (S. I. Smith)	Temperate-mesohaline
Neopanope sayi (S. I. Smith)[a]	Temperate-mesohaline
Panopeus herbstii A. Milne Edwards	Temperate-tropical-mesohaline
Rhithropanopeus harrisii (Gould)	Temperate-oligo-mesohaline
Subfamily Menippinae	
Menippe mercenaria (Say), Stone crab	Warm temperate-subtropical-mesopolyhaline
Family Grapsidae	
Subfamily Varuninae	
Hemigrapsus nudus (Dana), Purple shore crab[a]	Temperate-polyhaline
Subfamily Sesarminae	
Sesarma cinereum (Bosc), Wharf crab[a]	Temperate-tropical-polyhaline-semiterrestrial
Sesarma reticulatum (Say), "Marsh crab"[a]	Temperate-polyhaline-semiterrestrial
Superfamily Ocypodoidea	
Family Ocypodidae	
Subfamily Ocypodinae	
Uca minax (Le Conte), Red jointed fiddler	Temperate-oligo-mesohaline-semiterrestrial
Uca pugilator (Bosc), Sand fiddler	Temperate-subtropical-mesopolyhaline-semiterrestrial
Uca pugnax (Smith), Mud fiddler	Temperate-mesopolyhaline-semiterrestrial

[a]Species intimately associated with communities reported here and pollution studies published elsewhere.

III. Normal Life History–Ecology

Brachyuran crabs are dioecious, mating as adults. All have a complex ontogeny, passing through embryonic stages in eggs spawned by the female and borne by attachment to her pleopods until hatching into free swimming larvae, or zoeae, quite unlike the adult. The zoeae, released in waters of the meso- to euhaline range of salinity, depending on species, undergo a series of molts before reaching an intermediate stage, the megalopa, sometimes called the postlarva. The megalopa metamorphoses into the first crab stage, which is followed by successive molts until an adult stage is reached. Laboratory culture methods elaborated in the past 25 years have advanced knowledge of larval development in decapod crustaceans to the point that specific larval sequences not only can be described but also can be studied experimentally. The indispensable element in these techniques was discovery of a suitable diet for the larvae (Broad, 1957), the one almost universally used being freshly hatched nauplii of the brine shrimp, *Artemia salina*, occasionally supplemented or replaced by fertilized sea urchin eggs, rotifers (*Brachionis*), and, rarely, wild plankton (Sulkin and Epifanio, 1975; Sulkin and Norman, 1976). Postlarval stages, always easier to manipulate, have not posed such a feeding problem. The life history–ecology of all species discussed below is known from field and laboratory studies.

A. Family Cancridae

Twelve species of *Cancer* occur in waters of the Continental Shelf of America north of Panama. Distribution of the group is limited to cold or cool temperate waters (Nations, 1975). Only two species are reviewed here. These are the Atlantic rock crab, *C. irroratus* Say, and the Pacific Dungeness crab, *C. magister* Dana. The first ranges from Labrador to off Miami, Florida, to a depth of 575 m, the second from Amchitka, Aleutian Islands, Alaska (Hoopes, 1973), to Magdalena Bay, Baja California (Waldron, 1958), and from the low tide mark to about 90 m. Both are primarily marine species, normally entering estuaries only in their lower or high salinity regions.

Cancer irroratus has limited value in commercial fisheries (1.4 million lb in 1974) (Bell and FitzGibbon, 1977), and *C. magister* provides a considerable fishery (over 23 million lb, 1971–1975 annual average) (Robinson, 1977).

The species have similar life histories. Sexually mature hard males mate with sexually mature females somewhat smaller than themselves (Scarratt and Lowe, 1972), each such mating male carrying a female in a courtship embrace before, during, and after she molts into a terminally mature phase, the pair copulating when she is in the postmolt soft condition (Hartnoll, 1969; Snow and Nielsen, 1966; Butler, 1960; Poole, 1967). The mating season for *C. magister* extends from late February to August in California, but ovigerous females are known

nearly year round (Waldron, 1958); mating for *C. irroratus* extends through about the same period to October (Scarratt and Lowe, 1972), being seasonally timed at different latitudes, with shortened duration at the extremes of the range. Larval life of five zoeal stages and a megalopa last about 4 months (Poole, 1967; Sastry, 1977). The larvae of *C. irroratus* have been recorded in estuarine plankton by a number of workers (Sandifer, 1973), always in regions of high salinity. In the case of this latest survey, low concentrations occurred occasionally in lower Chesapeake Bay Stations, most abundantly off the mouth of the Bay in water of 23.3–32.3‰ salinity (mainly 25‰) from May to July and September to October, with one peak in May and a smaller one in October, mainly in the temperature range 13°–21°C. Sandifer (1975) felt that larvae of this species showed no distributional adaptations for retention in bays, as do larvae of some other species more or less restricted to estuarine habitats. Experimentally reared larvae survived best in 30‰ salinity at 15°C (Sastry, 1977), in 26–30‰ salinity at 10.6°C (Poole, 1966), and the most successful molt of a prezoeal stage in 30–32‰ salinity at 10.5° and 17.5°C (Buchanan and Millemann, 1969). Reed (1969) found that survival of *C. magister* larvae in culture was not significantly affected by temperatures and salinities approximating ocean ranges of these variables found within 40 miles of the Oregon coast during the zoeal period (optimally 10.0°–13.0°C, 25–30‰ salinity) but that reduced temperature and current transport might affect survival.

Both species may migrate into shallow high-salinity areas after the larval stages are past. Jeffries (1966) found *C. irroratus* in Narragansett Bay on sandy bottom; there was little mixing with populations of a companion species, *C. borealis*. Others have not found such clear separation of the latter two species on the Continental Shelf, but have noted some substrate selection (Musick and McEachran, 1972; Haefner, 1976); and Turner (1953, 1954) discussed seasonal aspects of distribution for Boston harbor as did Winget *et al.* (1974) for Lewes, Delaware, harbor. Jeffries noted that *C. borealis* has proportionately heavier chelae than *irroratus*, is less prone to burying in sand when disturbed, and generally shows a lower walking and activity rate, which he correlated with differences in serum phosphate concentrations possibly related to level of energy metabolism. Serum nitrogen, chloride, and glucose were also assayed. Comparison of walking ability in a treadmill showed *C. irroratus* to react optimally at 14°–18°C. *Cancer magister* prefers sand or sandy mud bottom, but may be found on a variety of substrates (Waldron, 1958).

Cancer is a predator (Squires, 1965; Mann, 1973; Caddy, 1973; Cornick and Steward, 1968) in turn preyed upon by fishes (Sikora *et al.*, 1972; Waldron, 1958) and the American lobster, *Homarus americanus* (Squires, 1965; Evans and Mann, 1977). There is considerable difference in size between the Pacific and Atlantic species, *C. magister* males reaching commercial size in 4 years (48–60 mm width in Oregon) and probably attaining a maximum age of 8 years

(maximum width about 220 mm) (Waldron, 1958; Butler, 1961). Less definite evidence on age is available for the Atlantic crab, distribution of sizes in one set of samples (Haefner, 1976) for *C. irroratus* falling into two modal sizes for each sex correlated positively with depth (<50, 51–100, and for males a third group up to 127 mm) but none approaching the size of of large *C. magister*.

At molting of *C. irroratus*, most water uptake occurs between peeler and soft crab stages when progressive growth in length, width, and weight results in increases of 18–23, 19–27, and 52–82%, respectively (Haefner and Van Engel, 1975). In tank experiments, crabs acclimated at 7°C approached isosmoticity near 28–30‰ salinity; crabs acclimated at 17.5°C were isosmotic near 24–26‰, but showed hyperregulation in less than 20‰ salinity. Beers (1958) concluded from structure of the green gland in *C. borealis* that its function is inefficient in salinities below 50% seawater, and hence limiting to estuarine tolerance of the species.

Experimentally, oxygen uptake in *C. magister* is independent of ambient O_2 tension down to about 50 mm Hg; further decrease caused a drop in O_2 uptake, but the crabs can endure exposure to tensions as low as 30 mm Hg for at least one-half hour (Johansen *et al.*, 1970). Such low conditions are probably never encountered naturally. Extraction of oxygen from water passed over the gills averages 16%.

In temperature tolerance experiments, Vernberg and Vernberg (1970) found that *C. irroratus* collected from the Cape Hatteras area in February died after 1 hour in water of 30°C, that many animals died after 2 hours at 32°C, but that animals were unaffected by 48-hour exposure to 10°C. Zoeae exposed to 4°C in 30‰ salinity survived for long periods with no harm, but zoeae at 20°C in water of 10‰ salinity were inactive after 1.5 hours.

Other aspects of the biology, such as functional organization of proprioceptors and hormonal control of chromatophores, are beyond the scope of this chapter.

B. Family Portunidae

Two species of the swimming crab family Portunidae are preeminent in the literature of biological research on estuarine species. *Callinectes sapidus* Rathbun, the blue crab, for which there is a major fishery in the United States (over 141 million lb, 1971–1975 annual average) (Robinson, 1977) and an undetermined catch harvested in Central and South America, has the most extended distribution of any member in its genus. The native range, occasionally Nova Scotia, Maine, and northern Massachusetts to northern Argentina, including Bermuda and the Antilles, has been extended by introduction to northwestern Europe, the central and eastern Mediterranean Sea as well as the western Black Sea, and to Lake Hamana-ko, central Japan (Williams, 1974, review; T. Sakai, personal communication). The green or shore crab, *Carcinus maenas* (Lin-

naeus), having a minimal commercial value (Bell and FitzGibbon, 1977), is thought to have been introduced in North America, where it ranges from Northumberland Strait, Canada, to Virginia, and in Australia. Its native range extends from Norway, just beyond 70°N, southward through the southern Baltic Sea, the North Sea, and the British Isles to the Straits of Gibraltar. A close relative, *C. mediterraneus* Czerniavsky of the Mediterranean Sea, has often been considered a subspecies (Christiansen, 1969; Rice and Ingle, 1975). Though both the blue and green crab live in shallow water, their biology is distinct. Our ecological review represents only a facet of knowledge concerning them, which has otherwise been reviewed by Waterman (1960, 1961), Crothers (1967, 1968, 1969, 1970), Clay (1965), Tagatz and Hall (1971), and Williams (1974).

1. Callinectes sapidus

Callinectes sapidus lives from the water's edge to 35-m depths, occasionally 90 m, in fresh water to salinities as concentrated as 117‰; large males have been taken from salt springs over 180 miles from the sea in Marion County, Florida. The species is known to tolerate summertime mean daily O_2 tension as low as 0.08 mg/liter in 1-m-deep experimental estuarine tertiary sewage treatment ponds in North Carolina (Williams, 1974, review), but crabs confined in baited pots in Chesapeake Bay showed stress when O_2 concentrations were less than 0.6 mg/liter at temperatures above 28°C (Carpenter and Cargo, 1957).

The species leads a migratory life, developmental phases being adapted to an estuarine–marine–estuarine cycle. Mating in North America may occur from May to October, usually in estuaries of reduced salinity, each sexually mature hard male carrying a sexually mature female in a courtship embrace before, during, and after she molts into a terminally mature phase. The pair copulates when she is in the postmolt soft condition (Churchill, 1919; Van Engel, 1958). Such females spawn in 2, or if winter intervenes, up to 9 months after migrating to higher salinity areas near the sea where incubation and hatching occur (Van Engel, 1958). Males remain behind. The eggs hatch in about 15 days at 26°C (Churchill, 1919). Larvae develop through seven zoeal stages, atypically an eighth, and a megalopa (Costlow *et al.*, 1959; Costlow and Bookhout, 1959), the staging and duration of development varying over a period of 31 to 69 days (Costlow, 1965, 1967). Development progresses at comparable rates in salinities between 20.1 and 31.1‰. Above 31.1‰ development is slowed, and below 20.1‰ larvae rarely complete the first molt. Several workers have shown that the zoeae move considerable distances to sea over the Continental Shelf (Nichols and Keney, 1963; Tagatz, 1968; Sandifer, 1973), but that return to estuaries may be largely as megalopae (Williams and Deubler, 1968; More, 1969; King, 1971; Williams, 1971; Naylor and Isaac, 1973) and young crabs (Van Engel, 1958). The megalopal stage lasts 6–20 days, and this stage is found in plankton more or less year round. Most of the off- and onshore movement appears to be a normal

developmental feature, but longshore larval transport obviously leads to temporary dispersal extensions at fringes of the range. Back within estuaries the young crabs undergo 18 to 20 molts before reaching maturity about 14 months later (Van Engel, 1958), and maximum age attained is estimated to be 3 years. Most movement of adults seems to be confined within estuarine systems (Fischler and Walburg, 1962; Tagatz, 1968), but there are exceptions (Leahy, 1975).

Kalber (1970) showed that the early zoeae are good osmoregulators, that the late zoeae lose this ability, and that the megalopae, though poor regulators at first, become good ones by the fifth day, the osmoregulatory adaptations apparently being fitted to the sequence of salinity stresses normally experienced during development. Ability to invade fresh water is governed by adaptation to chlorinity, the crabs being able to adjust to lowered levels if changes are experienced slowly, as in the case of migrations (Odum, 1953). Osmoregulatory ability of adult males and females is essentially the same, hypersomotic in 5 and 50% seawater but hyposmotic in 100% seawater (Tagatz, 1969, 1971; Engel, 1977). Growth increment of females during the terminal molt shows no significant correlation with salinity (Haefner and Shuster, 1964).

The usual diet of postlarval *C. sapidus* includes fishes, gastropods, *Littorina*, oysters, clams, mussels, tunicates, miscellaneous benthic invertebrates, and plant material (Darnell, 1959, 1961; Dunnington, 1956; Menzel and Hopkins, 1956; Tagatz, 1968; Hamilton, 1976; Odum and Heald, 1972; Pearson and Olla, 1977). The species is not expressly a scavenger, as often claimed.

Fluctuations in population density are reflected in commercial fishery statistics. Pearson (1948), analyzing possible relationships of measurable environmental factors to catch, concluded that the greatest single influence on success of a year-class may be salinity. The species needs high-salinity estuarine water for optimum hatches. Ovigerous females in river–bay–lagoon systems seem to have more successful hatches in years when river runoff is low. Experimental evidence from the larval studies supports this view.

2. *Carcinus maenas*

Carcinus maenas lives in depths of usually less than 5 or 6 m, but rarely descends to 200 m, on a variety of substrates (Christiansen, 1969). There is some migration in the shallows (Naylor, 1960), crabs <35 mm wide remaining below low tide in all months of the year, and larger crabs tending to move upshore with high tides in summer to remain stranded beneath stones at intervening low tides, but with no such movements in winter. Passive water loss from the gills tends to cool crabs subaerially exposed to high temperatures, helping to promote their survival (Ahsanullah and Newell, 1977). The species lacks noticeably flattened fifth swimming legs so characteristic of most portunids. Crothers (1969, 1970) found variation in population density associated with habitat, with lower densities occuring on wave-beaten, exposed shores, and higher concentrations pre-

vailing in protected bays with lowered salinity. The normal salinity range of the species is about 10–33‰.

Early molting of males may be correlated with the fact that hard males mate with females in the soft condition (Hartnoll, 1969), and hence would precede molt of the latter. Mating resembles that described for *Callinectes sapidus*, and may last for hours and be repeated if the pair is separated (Cheung, 1966, and others). Reaction of males to a displaying female may vary from pairing to rejection with injury to the female, probably depending on physiological state of the male. A single mating can fertilize more than one batch of eggs, but few soft females fail to mate. Females lack a terminal molt.

In Holland, the number of ovigerous females declines to near zero during the late summer–early fall molting period but abruptly thereafter rises to a level of 50–60% (Broekhuysen, 1936). This number persists through winter until June, when another brief drop occurs followed by some new spawning in July. These fluctuations correspond to phasing of maturity among females. Those that spawned in fall drop hatching eggs in the spring, molt, and then may cast a second clutch of eggs in summer. Overwintering juveniles may attain maturity in spring and spawn after that in early summer, but spawning varies from this pattern in other geographic areas. In the Baltic, berried females hide in deeper (8–10 m), more saline water until the larvae are hatched (Rasmussen, 1959). A large female (46 mm wide) is estimated to have 185,000–200,000 eggs in a clutch.

Experimentally, eggs will develop in a salinity range of 25.8–26‰ to 40.3–50.4‰ at 10°C, 41–53.1‰ at $\bar{x}$ 16.3°C, and 20‰ at 15.7–17°C. Cold of 1.4°C in low salinity areas kills eggs; the animals usually migrate to avoid such extremes. Upon hatching in darkness (Dries and Adelung, 1976), developing larvae pass through a sometimes abnormal prezoeal stage, four zoeal stages, and a megalopa (Williams, 1968; Rice and Ingle, 1975) in a little under 60 days at 15°C. In the western Atlantic, Deevey (1960) found larvae in Delaware Bay from June to August, and Hillman (1964) reported them from July to August and December in Narragansett Bay. Kurian (1956), finding larval occurrence in Europe correlated with temperature, reported larvae present the year round at Plymouth, but most abundant in spring and summer, while in The Sound off Norway they are present in summer, with megalopae persisting until fall. Rasmussen (1973) found that eggs spawned later than May–July may never develop to first crab off Denmark and that annual fluctuation in salinity–temperature governs success or failure of a year-class in those waters. Experimentally, *C. maenas* zoeae show a higher mortality in diluted seawater than megalopae, and metamorphosis of the latter is delayed or prevented by water of low salinity (Lance, 1964).

The green crab is an omnivore whose feeding is influenced by abundance, size, and kinds of food available (Ropes, 1968). Pelecypods formed a dominant part of the diet of crabs 30–59 mm wide in Plum Island Sound, Massachusetts,

which opened and ate clams equal to their own width, only the largest clams resisting attack. Greater amounts of food in crabs caught during low tide and just after sunrise suggested that feeding is heaviest at night and at high tide. Activity and feeding seem reduced at water temperatures below 7°C; low salinity apparently did not influence feeding. Ovigerous females were relatively inactive, thus less destructive of clams than nonovigerous females, as were mating males and crabs either preparing to molt or assuming a new hardened integument. The green crab has had an economic impact on the fishery for the soft clam, *Mya arenaria*; decreases in the fishery, especially from clam farming, have been correlated with its predation (Glude, 1955). A marked increase in the soft clam fishery of New England has been linked to mortalities and declining abundance of this crab, which have been associated with cold winters and a general cooling trend (Welch, 1968).

In normal seawater there is active absorption of water by the crabs, but in dilute media this is suspended when osmoregulation begins, and possibly there is a fall in passive permeability of the gills to water (Webb, 1940). Ionic regulation is a resultant of the following processes: active absorption by the gills of Na, K, Ca, and chloride at a rate greater than that at which they are lost by diffusion; differential excretion by the antennary gland, which tends to conserve K and eliminate Mg and SO_4; and inward diffusion of Mg and SO_4 across the gills in accordance with concentration of the gradient.

C. Family Xanthidae

The Xanthidae, richest in species of all crab families, are represented in North American estuaries by six species, about which some understanding of pollution effects is known. The common name "mud crabs" can be applied to part of these with some justification (Table I) but not to all. Differences between species groups are extensive—encompassing structure, reproduction and larval development, behavior, and physiology, and it is useful to recognize subfamilies.

1. Subfamily Xanthinae

Aside from distinctive niches and geographic ranges of the species in this group, enough biological features are shared that they can be generalized under the last species in the series.

Cataleptodius (=*Leptodius*) *floridanus* (Gibbes) (see Chapter 8, p. 264) ranges from Bermuda, the Bahamas, and the Florida Keys to São Paulo, Brazil, on a variety of reefs and other substrates in shallow water (Rathbun, 1930; Guinot, 1968; Hazlett *et al.*, 1977).

Eurypanopeus depressus (Smith) ranges from Massachusetts Bay through east and west Florida to southern Texas, as well as Bermuda, the West Indies, and Uruguay (Williams, 1965). It is abundant on oyster bars in a recorded salinity

range of 4.5 to 20.4‰ in Chesapeake Bay (Ryan, 1956), and has been recorded in similar habitats elsewhere in depths to 48 m.

Neopanope sayi (Smith) (=*N. texana sayi*) (Abele, 1972) ranges from Chaleur Bay, New Brunswick, and Cape Breton Island, Nova Scotia, Canada (Bousfield and Laubitz, 1972), to the Florida Keys (Abele, 1972), and has been introduced in Wales (Naylor, 1960). It frequents mud or oyster shell bottoms, as well as sea grass beds (Ryan, 1956; Marsh, 1973), from the low tide mark to 46 m.

Panopeus herbstii A. Milne Edwards ranges from Bermuda and Boston, Massachusetts, to Santa Catarina, Brazil (Williams, 1965). It has been introduced in Hawaii and has supposedly long been seen on western U. S. shores (Edmondson, 1962). The species inhabits a number of nearshore substrates—predominantly mud, shell, or stones, from the intertidal zone to 22 m and over a broad range of salinities.

Rhithropanopeus harrisii (Gould) presumably had a native range extending from the southwestern Gulf of St. Lawrence, Canada, to Veracruz, Mexico, and it has been introduced on the West Coast of the United States (Williams, 1965). An older and wider introduction in northwestern Europe, the Black Sea, Sea of Azov, and Caspian Sea is often regarded as a distinct subspecies, the Holland crab (Christiansen, 1969; Gadzhiev, 1963; Makarov, 1977). The hardy species thrives in a very broad range of salinities, an attribute that enhances the ease with which it has been transported and introduced; and with which it can be manipulated in laboratory experiments. More is known about at least the larval development of this species than any other in the subfamily.

Larval development of species in the subfamily Xanthinae includes four zoeal stages and a megalopa. Connolly (1925), using plankton, and Chamberlain (1962), using laboratory culture, demonstrated this for *R. harrisii*. Christiansen and Costlow (1975) reared the species from hatching through the first or second crab stages under experimental conditions in 11 combinations of salinity and cyclic temperatures (5, 20, 35‰ salinity at 20–25°, 25–30°, 30–35°C; and 25‰ S at 20–25° and 30–35°C). Larvae survived to megalopa plus first crab in all combinations except 5‰ salinity at 30–35°C. Best survival to megalopa (94%) and first crab (90%) was obtained in 20‰ salinity at 20–25°C. In all other combinations there was a reduction in survival to the first crab stage. Duration of larval stages was affected significantly by temperature, whereas the effect of salinity on mean days from hatching to the first crab was not consistent in different temperature cycles. The authors concluded that larval development of *R. harrisii* is strongly influenced by environmental factors and not solely related to genetic differences. Earlier, Costlow *et al.* (1966) found that time of development was not significantly affected by salinities of 5–35‰ in noncycled temperatures and suggested that the capacity to develop normally within this broad range of environments may have contributed to the wide distribution of the

species. Aspects of osmoregulatory ability are comparable to those discussed for *Callinectes sapidus* (Jones, 1941; Kalber and Costlow, 1966, 1968; Capen, 1972), and Smith (1967) showed that inward permeability to water is decreased at lower salinities.

Ovigerous females occur during the warm months in Chesapeake Bay (Ryan, 1956). Zoeae are present from May to October in tributaries of the Bay, with peak occurrence from June to July (Herman *et al.*, 1968; Sandifer, 1973), the latter finding them common to abundant in 0–10‰ salinities but less abundant in the Bay proper. Others have shown similar occurrences elsewhere with some adjustment for latitudinal temperature differences (Bousfield, 1955; Tagatz, 1968; Williams, 1971). Sandifer (1975) contended that stratification of the larvae on bottom indicates that their retention in estuaries is the major means of recruitment for the species.

Ryan (1956) judged maturity to be reached in about 1 year, but molting and growth continue throughout life. Maximum carapace widths are about 21 mm for males and 16 mm for females. Maximum age has not been estimated.

Success of *R. harrisii* in the estuarine environment is emphasized by its abundance and role in the food web. Odum and Heald (1972) found more than 40 animals per square meter in holes, under leaves, logs, shells, and other debris in the bed of an estuarine stream draining a *Juncus* marsh in south Florida. The omnivorous diet was dominated by mangrove leaf detritus. Crustaceans such as small amphipods and harpacticoid copepods were eaten more often by small crabs. The crabs are preyed upon by hakes (Sikora *et al.*, 1972), the white catfish (Heard, 1975), and probably other predaceous fishes.

What is known of the life histories of other xanthines helps to round out knowledge of them collectively. Mating pairs of *Neopanope sayi* have been observed in laboratory tanks supplied with running seawater at Gloucester Point, Virginia, from late March until early September. Females mate in the hard condition, occasionally when ovigerous, and both sexes may copulate several times during a molt cycle (Swartz, 1972). The reproductive season is judged to be governed by temperature, mainly in the 24°–30°C range. Ovigerous females have been observed from April in South Carolina (Lunz, 1937) to October in Chesapeake Bay. Eggs hatch in about 10 days. Chamberlain (1957, 1961) discussed larval development, finding that it varied with temperature (14 days at 30°C, 27 days at 21°C) and food, as did Sulkin and Norman (1976). Sandifer (1973) found zoeae in lower Chesapeake Bay from June to October but concentrated in June, mainly in 20–25‰ salinities, and he summarized latitudinal variations in planktonic occurrence found by others from Narragansett Bay to Florida, emphasizing his (1975) view that retention in estuaries is reinforced by stratified densities and circulation. Swartz (1972) concluded that the crabs mature in 1 year and that some individuals survive to an age of 2 years.

Neopanope sayi is a predator on oysters, the barnacle *Balanus improvisus*, and young *Mercenaria mercenaria* clams (McDermott and Flower, 1952; Landers, 1954). In turn it is preyed upon by fishes.

Panopeus herbstii roughly parallels *N. sayi* in life history details. It is a species to which Costlow *et al.* (1962) early applied the idea of response surface analysis in an attempt to describe optimum conditions for larval development, hypothesizing that effect of temperature on successive larval stages limits the productive spawning period. Low temperatures favor the spring brood of larvae, prolonging larval development until warmer water produces favorable conditions for the megalopa, whereas larvae hatched in fall are not so favored and therefore suffer higher mortalities. Among various marsh crabs in Georgia, only *P. herbstii* was found active at temperatures below 12°C (Teal, 1959).

Menzel and Nichy (1958) found that, among xanthids only *P. herbstii* and *Menippe mercenaria* were large enough to kill significant numbers of adult oysters. McDermott (1960) concluded that *P. herbstii*, preying on oyster spat as well as barnacles (*Balanus improvisus*), is potentially the most destructive of five species of mud crabs on New Jersey oyster beds.

Walton and Williams (1971) studied populations of *Eurypanopeus depressus* on artificial reefs in three small experimental estuarine ponds in North Carolina, finding it to be the most abundant species of xanthid following heavy seeding with estuarine plankton a year before. The crabs matured in the ponds, 50% of females in one pond being gravid when sampling began in late June. This percentage remained high in samples during the summer, once being 100% for an estimated population of 276. There was gradual reduction in gravid females after the end of August. The size range in samples from Chesapeake Bay suggested to Ryan (1956) that maturity might be reached in the first summer after eggs have hatched and that molting continues after maturity is reached. Sandifer (1973) found larvae of this species only three times during his plankton survey of lower Chesapeake Bay, but others (Pinschmidt, 1964; Dudley and Judy, 1971), including authors cited above, have found them throughout the warm season. McDermott (1960) considered the species a predator on oyster spat in southern New Jersey but not so serious a pest as *P. herbstii*.

2. *Subfamily Menippinae*

The stone crab, *Menippe mercenaria*, stands alone among the xanthid crabs in size, fishery value, and reproductive specializations. It ranges from the Cape Lookout, North Carolina, area to Yucatan, Mexico, the Bahamas, Cuba, and Jamaica, the crabs shifting among various environments as they grow. The maximum recorded depth of occurrence is 51 m. The youngest crabs are found under shell fragments or in crevices among rocks in deeper saltier estuaries, or in fouling on buoys. Older crabs may be found more shallowly among oyster shells,

in fouling about jetties, etc., or in turtle grass. There they live until nearly grown, when they may move to shoals to construct burrows, some apparently colonial, as much as 75 cm in length, just below the tide mark. But adults are also found on oyster reefs, among rocks along jetties, and on offshore reefs or wrecks (Williams, 1965, review; Powell and Gunter, 1968).

About 2.5 million lb of stone crabs were landed in Florida in 1974 (Bell and FitzGibbon, 1977), although unrecorded catches for home use are known elsewhere as well. The flesh is considered a delicacy.

Reproduction in *M. mercenaria* has been a subject for active investigation since early in this century. Savage (1971) observed and described mating of a male and female held in an outdoor aquarium. Both then and among mating pairs observed in the field, males were always with freshly molted or presumed freshly molted females. Females in laboratory experiments have produced more than 10 broods of viable eggs within the same intermolt over a 120-day period without copulation taking place in intervals between production of the different broods (Cheung, 1968; Yang, 1971), the interval between hatch of one brood and oviposition of the next being 2–3 days. Eggs of all these broods were successfully attached to hairs of pleopods and developed to hatch as normal zoeae. Moreover, females from the wild held in isolation through a molt were found to retain sperm through ecdysis, a special adaptation (late disposal of the old invaginating exoskeletal wall between sperm and new wall) enabling retention. Cheung (1969) also showed that ovarian development is closely correlated with water temperature, optimum development being at 28°C. Seasonally, spawning built to a peak from August to September in southern Florida, but dropped to a low in winter. Elsewhere, ovigerous females are known from May to August in North Carolina and August in Texas (Powell and Gunter, 1968).

Porter (1960) described larval development, including a prezoeal and six zoeal stages, but he considered the first and last of these to be atypical. Ong and Costlow (1970), with much more sophisticated equipment, reared larvae in 18 environments (six salinities, three temperatures). Both factors were found to affect rate of development and survival, optimal conditions being about 30°C in 30–35‰ salinity in which the megalopa was reached in 14 days and the first crab in 21 days with survival of 60–72%. Development was slower in both lower temperature and salinity. Yang (1971) successfully reared mass and individualized cultures, showing that there were five zoeal stages and a megalopa. Dudley and Judy (1971) found stone crab larvae in plankton off Beaufort Inlet, North Carolina, from June to August. Mootz and Epifanio (1974) determined an energy budget for larvae fed *Artemia salina* nauplii, and found that larval growth is exponential during zoeal stages but decreases during the megalopa even though consumption reaches a peak during this stage.

These crabs are powerful and active predators, feeding on large and small oysters (Menzel and Hopkins, 1956), barnacles (Powell and Gunter, 1968),

gastropods, etc. The fingers of the chelae, if fastened upon a hard object, can hardly be pried apart; the strength of this grip by one male on a hard object was so great that it crushed its own chela and bled to death. Powell and Gunter judged stone crabs to have a strong influence on the life of sand and mud flats that are exposed by wind or lunar low tides because their water-filled burrows are refuges for small aquatic organisms that cannot withstand drying. Commensals found in burrows include sea anemones, tube worms, bivalve and gastropod mollusks, barnacles, amphipods, caridean and brachyuran decapod crustaceans, and fishes, to name a few.

D. Family Grapsidae

Three species of Grapsidae considered here all live in the intertidal zone, two in marshlands of the eastern and southern U. S. coast, and the third along beaches of western North America. Considerable divergence in ecology is hidden under systematic similarities; therefore the species are discussed separately.

1. Subfamily Varuninae

Hemigrapsus nudus. The purple shore crab ranges from Yakobi Island, Lisianska Strait, Alaska, to the Gulf of California (Hart, 1968). The species lives mainly in upper reaches of the intertidal zone on well-drained substrate, such as boulders situated over coarse sand or broken shell, in contrast to a smaller relative, *H. oregonensis,* which lives lower down on siltier substrate (Knudsen, 1964, review). The adults are herbivorous, gleaning microalgae from rocks, mainly at night, by the large chelae, although gut contents include some sand and incidental animal matter.

Mating pairs (both sexes in hard condition) occur in Washington from early December to early February (Knudsen, 1964), and ovigerous females are reported there and elsewhere from October to July (see also Boolootian *et al.*, 1959). There is almost no evidence of a second brood. Hart (1935) described five zoeal stages, the megalopa and first crab stage from laboratory rearing on a diet composed mainly of *Ostrea lurida* Carpenter larvae, and thus there is change in diet during maturation.

Aspects of the species' physiology have been studied at length in the last quarter century. Dehnel (1962) demonstrated the inability of *H. nudus* to hyposmoregulate and demonstrated further a seasonal variation in regulatory ability. Hyperosmotic regulation in dilute salinities in summer is achieved by extra-renal mechanisms, for the blood and urine are isosmotic. Hyperosmotic regulation in winter, however, is accomplished by production of urine less concentrated than the blood, suggesting ion reabsorption by the kidney (Dehnel, 1966; Dehnel and Stone, 1964). Size had no effect on osmotic response and weight remained stable during experiments. Dehnel, further elaborating seasonal changes in ionic bal-

ance, showed that salinity affects metabolic response to temperature; oxygen consumption is highest in low temperature–low salinity combinations (Dehnel, 1960, 1966), the response being thought to result from work to maintain osmotic balance. In experiments, acclimation (1 week) to high temperatures generally increased resistance to lethal temperatures whereas acclimation to low salinity decreased it (5°C, 35% seawater, 50% survived at 28.81°C and 28.68°C for 12 and 24 hours, respectively). High temperature–high salinity (20°C, 75% seawater) was the most favorable combination for withstanding the high test temperatures (50% survival at 34.32°C and 33.45°C for 12 and 24 hours, respectively) (Todd and Dehnel, 1960). Blood glucose has been determined at relatively low levels (0.75–2.55 mg/100 ml), varying to some degree with molt cycle (McWhinnie and Scheer, 1958), but on the whole is relatively stable through changes in diet and season (Meenahshi and Scheer, 1960), although its precursors vary.

2. *Subfamily Sesarminae*

a. Sesarma cinereum. The wharf crab, wood crab or square-backed fiddler crab, ranges from the Magothy River, Chesapeake Bay, Maryland, to Palm Beach, Florida, and from Collier County, Florida, to Veracruz, Mexico (Abele, 1973), and is absent from extreme southern Florida. The crabs inhabit supralittoral zones of marshes characterized by high salinity ($\bar{x}$=27.9‰) and sandy substrates (Seiple, 1979), actively crawl about on wharves and jetties or rest in shallow burrows above tidemark along shores, and have often been found on vessels along the coast, hiding by day and coming forth at night to search for food.

There is little recorded information on food habits. Seiple (1979) showed that the species eats *Spartina* shoots in the same manner as that recorded by Crichton (1974) for *S. reticulatum*. Oler (1941) maintained captives for about 1 year in an aquarium on mud substrate, with tap water as moisture and vegetable matter as food, but the larger crabs cannibalized smaller crabs in the group, presumably at ecdysis.

Ovigerous females are known from January along the Potomac River (Williams, 1965), and mid-April (Seiple, 1979) to November in North Carolina. Females in North Carolina produce four to six egg batches in close synchrony with lunar phase, each female carrying her eggs approximately 1 lunar month, with peak reproductive activity occurring from April to June (Seiple, 1979). From summer hatchings, Costlow and Bookhout (1960) found that larvae fed *Artemia salina* nauplii passed through four zoeal and a megalopal stage before metamorphosis. Costlow *et al.* (1960) found that optimum salinities exist for each larval stage, but that development proceeds best in the 20–26.7‰ salinity range. Temperature was found to have more effect on length of larval development than on mortality, with higher temperature speeding development, but the authors concluded that salinity is the chief physical factor confining *S. cinereum* to estu-

17

aries. Records of larvae from plankton vary with site of sampling. Pinschmidt (1964), in Newport River near Beaufort, North Carolina, found early zoeae in low concentration from June to September in water of 19°–34°C and 7–36‰ salinity, but most numerous in August at 25°–31°C. Sandifer (1973) found the larvae rarely in York and Pamunkey rivers, Virginia, in June and August, the samples being from bottom water of 24.8°–26.6°C in 11.9–19.64‰ salinity. *Sesarma* larvae occur from June to September up to 6.5 km off Beaufort Inlet, North Carolina (Dudley and Judy, 1971), and Tagatz (1968) found larvae of this genus to be the second most abundant form in samples from St. John River, Florida, from April to October, peaking in August. Sandifer (1975) applied his theory of estuarine retention to this as well as other species with similarly distributed larvae.

Teal (1959) implied that *S. cinereum* acts more like a land animal than an aquatic one because the species was relatively inactive under water in experiments, thus holding its oxygen consumption down. There was some experimental evidence for thermal acclimation of metabolism, but more evidence for acclimation by selection of microclimate. Gray (1957) showed that the gill area is nearly double that of another semiterrestrial species, *Ocypode quadrata* (Fabricius).

b. Sesarma reticulatum. This marsh crab is distributed from Woods Hole, Massachusetts, to presumably somewhere on the east coast of Florida, and from Sarasota on the west coast of Florida to Calhoun County, Texas (Abele, 1973). The species borrows communally in muddy salt marshes, its holes as much as 0.75 m deep and occasionally intersecting those of *Uca* species (Crichton, 1960; Allen and Curran, 1974). Teal (1959) found *S. reticulatum* active on Georgia marshes when the tide was high or the sky cloudy. When the marsh was exposed the crabs were in burrows, usually near the top in air or water. The diet is primarily *Spartina* (Crichton, 1974). The species occurs prominently in marsh ecosystems (Day *et al.*, 1973; Subrahmanyam *et al.*, 1976), often along with *Uca pugnax* and *minax* (Teal, 1958; Allen and Curran, 1974), functioning not only as a herbivore but also as a burrower that tills the land, increases erosion, and turns over the cord grass more rapidly than the annual decay cycle could do it.

From summer spawning, Costlow and Bookhout (1962) described a larval development of three zoeal stages and a megalopa in laboratory rearings on a diet of *Artemia salina* nauplii. Larvae have been taken sparingly in plankton of lower Chesapeake Bay and its tributaries (Sandifer, 1973) from June to October, most abundantly from July to August, in a temperature range of 22.8°–27.9°C and salinities of, rarely 10‰, usually 15–20‰, or more. Eighty percent of the larvae were taken at the bottom. Sandifer (1975) regarded this depth distribution as an adaptation for retention in estuaries. The functional basis of the adaptation may be a demonstrated hyperosmoticity of larval stages through early megalopa over a wide range of salinities, increasing density of the larvae (Foskett, 1977).

Foskett also thought this hyperosmoticity might act to provide turgor pressure within the thin larval cuticle whereas hard-shelled adults that hyperregulate in salinities below 27.5‰ but hyporegulate above this, as most crabs, have no need for such a mechanism.

Teal (1959) found respiration rates higher in water than in air. Teal and Carey (1967) found that *S. reticulatum* can regulate its metabolism down to about 6% atmosphere (45 mm Hg); however, marsh crabs do not encounter low oxygen conditions in air, only in burrows in water. There, during periods of submergence, the respiration rate may decline with decreasing oxygen pressure, and below critical pressures the crabs must convert metabolism to fermentation. Lactic acid is probably formed from glycogen, to be oxidized at the next period of emergence. Gray (1957) found the gill area of *S. reticulatum* to be relatively low compared to that of other species living in similar habitats (*Uca pugnax* and *minax*). He found *S. recticulatum* more robust but less active than its congener, *S. cinereum*.

E. Family Ocypodidae

Crane (1975), in her exhaustive monograph on fiddler crabs of the world, distilled years of study into a compendium of information on systematics, zoogeography, ecology, functional morphology, behavior, phylogeny, and evolution of the group. She recognized 79 species, many subdivided into subspecies, clustering them into a number of subgenera. Three of these species from the Western Hemisphere are so universally recognized in the biological literature as *Uca minax* (LeConte, 1855), *U. pugilator* (Bosc, 1802), and *U. pugnax* (Smith, 1870) that we feel constrained to retain this nomenclature, accepting taxonomic simplifications recommended by von Hagen (1976). His thesis is that any specialist will recognize these entities while appreciating the subtleties of variation, as did Crane, and that formal splitting seems premature and burdensome because attributes of the populations are still unclear and their importance has not yet been weighed.

Uca minax, the red-jointed fiddler, ranges along the eastern and southern coasts of the United States from the southern shore of Cape Cod, Massachusetts, to northeast Florida, and from the area of Yankeetown, northwest Florida, to Louisiana, and on to Matagorda Bay, Texas, if von Hagen's analysis treating *Uca rapax longisignalis* Salmon and Atsaides, 1968, as a synonym is accepted. *Uca pugilator*, the sand fiddler, ranges from Cape Cod, Massachusetts (rare on the north shore), southward around the tip of peninsular Florida and westward to Corpus Christi, Texas; single occurrences are on record from Old Providence Island, the Bahamas, and Santo Domingo. *Uca pugnax*, the mud fiddler, ranges from Provincetown, Massachusetts, to Daytona Beach, Florida. *Uca virens* Sal-

mon and Atsaides, 1968, from the Gulf of Mexico coast, considered a subspecies of *U. pugnax* by Crane, is synonymized by von Hagen with *U. rapax* (Smith, 1870), a tropical species ranging southward to southern Brazil.

Uca species live in an environmental borderland along the edges of estuaries, and habitually stay away from the sea proper. The crabs are behaviorally terrestrial but physiologically aquatic (Herrnkind, 1968b), orienting themselves within their narrow environment on the strand between water and land by visual cues, and able to return to it even if displaced several meters into either open water or to land beyond the beach. They exhibit endogenous rhythms in activity and color changes that are associated with local tidal schedules as well as diel cycles (Barnwell, 1968). All are burrowers, some retreating into more or less impermanent burrows during periods of inundation and emerging during low water stands. Of species discussed here, *U. minax*, the largest, lives on muddy banks of marsh creeks and among *Spartina*, *Salicornia*, and freshwater herbs in marshes threaded by brackish to freshwater streams under tidal influence (Miller and Maurer, 1973). *Uca pugnax*, medium sized, frequents salt marshes and sheltered shores on mud to sandy mud substrate. *Uca pugilator*, the smallest of the three, lives on sheltered shores with sandy to sandy mud substrate more or less free from vegetation and often mixed with scattered shells and stones but with muddy surfaces for feeding nearby. The food of all consists largely of minute particulate matter, algae, bacteria, detritus, etc., from the surface of the substrate which is scraped up by the small chelipeds and passed to the mouth for separation of accepted organic and rejected inorganic components by various mouthparts, the rejectamenta being left behind as trails of rounded pellets (Schwartz and Safir, 1915; Miller, 1961). Feeding underwater, however, has been observed for *U. pugnax* and *minax*, and the latter will kill and consume either of the other two species (Teal, 1958). Males, having only one small chela, feed twice as long as females, animals of each sex otherwise having equal metabolic responses (Valiela *et al.*, 1974).

Life histories of the three species are similar. Crane (1975) discussed courtship and mating in great detail, showing that males attract females by waving display and sound production, i. e., drumming the major hand against the substrate either on the surface or in burrows (Salmon and Horch, 1972), and that copulation in the hard condition (Hartnoll, 1969) takes place in the burrow of the male or, in *U. pugilator* and *pugnax*, on the surface at night, and even under water in captivity (Herrnkind, 1968a). Apparently the huge claw of the males is reserved for display (threat, attraction, etc.), not for handling females. Both sexes show a periodicity in gametogenesis (Young, 1974). Courtship and mating are influenced by temperature, with some evidence of latitudinal adaptation (Crane, 1975). Near New York, for example, *U. minax* fed and moved above ground during low tide in mid-June but did not display when air temperature during the

preceding night fell below 21°C, even though daytime temperature then regularly reached above 29°C. On Cape Cod in early June several *U. pugilator* waved at low intensities on a sunny day when air temperature was 19°C and the previous nighttime low had been 10°C. Maximum breeding activity for that population was in mid-June followed by notably less activity in July even though temperature was higher. Never was the activity on Cape Cod equivalent to that seen in more southern populations. Spawning following mating, therefore, is most extended at low latitudes. Ovigerous female *U. pugilator* have been reported from early July to mid-August on Long Island (Schwartz and Safir, 1915), March to midsummer in Virginia (Williams, 1965), April to October near Miami, Florida (Herrnkind, 1968a), and Hedgpeth (1950) reported zoeae taken in a plankton net on May 20 at Long Lake, Texas. Females enter the water to let eggs hatch.

Uca pugilator, representative of all, has five zoeal stages and a megalopa, each of these subdivisions of larval life lasting 3–4 weeks for a total development time of 6–8 weeks (Hyman, 1920; Herrnkind, 1968a). The larvae are predatory, capturing prey (*Artemia* nauplii, etc.) on or between the telson spine by violent flapping of the abdomen, whereupon flexure of the body brings food to the mouth. The megalopa swims at first but gradually adopts a benthic existence. Zoeae of the three species have not been distinguished in plankton, but Sandifer (1973) found zoeae of *Uca* sp. to be the most commonly collected and abundant decapod larvae in lower Chesapeake Bay, with concentrations of $>100/m^3$ not unusual. The zoeae were taken over a salinity range of 0.06–32.34‰ at temperatures of 19.4° to 30.8°C, but most numerously in the York and Pamunkey rivers tributary to the Bay, mainly at salinities <5‰ at 26°–30°C. Larvae first appeared in June, peaked in July, and disappeared in October. All of the zoeal stages were collected but stage I was most numerous, predominantly at the surface. Stage V was more numerous in bottom than in surface samples. Sandifer found that the work of others (reviewed) reflected his findings with allowance for latitudinal variation, although workers in the Beaufort, North Carolina, area found larvae at higher salinities (Pinschmidt, 1964; Dudley and Judy, 1971).

Recently Christy (1978) proposed that mating, incubation, hatching, and larval development in *U. pugilator* are synchronized with tides such that male display reaches peaks at spring tides, and mating occurs in male burrows where females remain during the entire incubation period of about 2 weeks, emerging to release hatching larvae at neap tides. Ensuing larval development is so timed that the megalopae will be ready to metamorphose when they are swept into the estuary on spring tides. There are thus two breeding populations allied with new and full moon tidal phases. Nonbreeding males and females, or displaying males, constitute the feeding droves that emerge at each low tide.

Further topics summarized below under the species in which they have been studied most include salinity and substrate associations, metabolic response to temperature, and other environmentally influenced physiological changes.

1. Uca pugilator

Most attention has been focused on the sand fiddler. The first two crab stages following metamorphosis are relatively weak and adapted to clinging, but following them the crab starts to assume the familiar structural and behavioral characteristics of the species, burrowing during high tides first in the wet intertidal area and later along the strand near or above the high tide line (Herrnkind, 1972). From that refuge the population emerges between high tides to carry on its activities in droves on the exposed intertidal surfaces. Rhythmic activities in such an environment follow naturally, but their behavioral complexities lie mainly beyond the scope of this chapter (see Crane, 1975). An example of internal rhythms is that of blood glucose level tied to the diurnal cycle, high in late afternoon, low in early morning. Example levels measured in percent milligrams are 5:30 AM, 7.86; 1:30 PM, 8.06; 5:30 PM, 15.41 (Dean and Vernberg, 1965).

Testing salinity tolerance, Teal (1958) found that 50% of *U. pugilator* died after 3.5 days in fresh water, but over 50% survived more than 10 days in seawater of 7‰ salinity. Given a choice of fresh water or seawater of 30‰ salinity, the crabs chose seawater but preferences of females were less strong than males, as was true of *U. pugnax*. He concluded that this species lies between *U. minax* and *U. pugnax* in its tolerance of fresh water, and can survive soakings of the *Salicornia* marsh with rain between spring tides.

Teal (1958) also concluded that *U. pugilator* cannot feed properly where sand is absent, because in choice of substrate experiments (sand or mud above or under water) it burrowed in sand above water and when restricted to an unfavorable low muddy marsh did not survive. In company of either of the other species, *U. pugilator* reduced its burrows in sand above water by 50%.

Respiration rates are higher underwater than in air (Teal, 1959) probably because of increased activity necessary to aerate the gills. Like *Sesarma*, this species and *U. pugnax* can regulate their metabolism in air under experimental conditions down to 1 or 2% atmosphere (8–15 mm Hg), but low oxygen pressures are encountered in nature only in burrows in water and there the crabs, like *Sesarma*, can go into oxygen debt until emergence at the next low tide.

Latitudinal effects of temperature are manifest in metabolic response. Rate of metabolism in a Massachusetts population was higher at 1.4°C than in a Florida population, but at 15°C the difference was not significant. The northern population was less sensitive to temperature change and more resistent to low temperature than the Florida population (Démeusy, 1957). Edwards (1950) earlier had shown metabolic differences in the populations at 20°C. Teal (1959) found that crabs from Georgia showed no adjustment of respiration for temperature acclimation above 25°C, but that below 20°C there was some evidence of acclimation though not so well developed as in *U. pugnax*. Summer temperatures of 45°C on open *Distichlis-Salicornia* flats in Georgia prevent *U. pugilator* from perma-

nently occupying these areas (Teal, 1958). Metabolic activity in *Uca* of the temperate zone exhibits a seasonal cycle and this cyclic change must be taken into account in comparing physiologic activity of relatives at different latitudes. Metabolic response of fiddler crabs has real significance in their distribution (Vernberg, 1959), manifesting itself to some degree even in the larval stages (Vernberg and Costlow, 1966).

Beyond respiratory responses, there is a significantly larger number of cells per unit volume and a higher titer of blood protein in *U. pugilator* at 30°C than at 10°C. Clotting time is significantly lengthened in the 10°C crabs (Dean and Vernberg, 1966). These physiological effects are associated with activity levels mediated by temperature.

2. Uca minax

The red-jointed fiddler, often found in *Spartina* marshes in the area immediately preceding the *Salicornia-Distichlis* zone (Vernberg, 1959) and occasionally at the edge of low woodlands, has lived in fresh water for more than 3 weeks (Teal, 1958), and when offered choice of fresh or seawater, chose fresh water. In choice of substrate experiments (mud or sand) it chose mud either above or under water, but dug few burrows when competitive *Uca* species were present.

Teal (1959) found *U. minax* to have the lowest rate of oxygen consumption among a number of marsh crab species (*U. pugnax* and *pugilator*, *Sesarma cinereum* and *reticulatum*, *Eurytium limosum*, and *Panopeus herbstii*). He (also Vernberg, 1959) showed that this species in all probability does not acclimate respiratory rate to changes in temperature. Moreover, its gill area per gram of body weight is lowest among U.S. East Coast *Uca* (Gray, 1957).

3. Uca pugnax

The mud fiddler's name derives from its preference for a muddy marsh environment, often well shaded (Schwartz and Safir, 1915), but it is perhaps somewhat excluded from areas where there is an abundance of halophyte roots or where substrate is too fluid to support burrows (Kraeuter and Wolf, 1974). Burrows can extend to depths of 60 cm (Pearse, 1914). Results of salinity tolerance experiments are consistent with this type of distribution (Teal, 1958); 50% of *U. pugnax* placed in fresh water died within 1.5 days, whereas 50% mortality occurred after 3 days in seawater of 7‰ salinity. Given a choice of fresh or seawater of 30‰ salinity, the crabs chose seawater.

As implied above, *U. pugnax* exhibits one of the most highly developed thermal adaptabilities among marsh crabs tested (Teal, 1959), and its abundance may be explained in part by its ability to regulate its metabolism over a wide range of temperature (Vernberg, 1959; Vernberg and Tashian, 1959).

IV. Pollution Ecology

Estuarine crabs occupy an ecological niche in the coastal environment that unfortunately is especially susceptible to man-made and natural pollutants. Sources of pollutants include industrial and municipal effluents entering rivers that transport the pollutants to the coastal environment—pesticides transferred by agricultural runoff, pesticides directly applied to control noxious insects such as mosquitoes, atmospheric exchange, and transported ocean-outfall discharge (Fig. 1). Whatever the source, pollutants can be concentrated in the crab's habitat, becoming part of the bottom sediment by precipitation, adsorption onto suspended or bottom sediments, and bioaccumulation. Conversely, pollutants can be diluted and dispersed by current and tidal action, biological transport, and vaporization. Recent surveys of pollutant residues in coastal zone organisms indicate that at least a portion of the pollutants entering this area is accumulated and often concentrated by estuarine brachyurans.

Crabs may be adversely affected by direct toxicity or indirect damages. Indeed, such influences can adversely affect a crab fishery if the amount of concentration in the species sought exceeds guidelines established by the Food and Drug Administration for seafood products.

For this discussion, we selected a few groups of pollutants of current interest to the scientific community: pesticides, heavy metals, oil, thermal discharges, and radionuclides. The list neither encompasses all groups of pollutants nor all the pollutants within a particular group; rather, it represents some of the major contaminants entering the crabs' environment.

A. Pesticides

Pesticides and other exogenous organics continually enter the marine environment through the atmosphere, river discharge, terrestrial runoff, and direct application. In many instances these materials, or their "breakdown" products, enter the biogeochemical cycles operating in the marine environment and are accumulated by organisms such as crabs. Often residues of these chemicals can be detected in the organism in minute (parts per trillion) concentrations by sophisticated analytical techniques, but their effect and their mechanisms of effect are essentially unknown. We do know, however, that pesticides are used to eliminate noxious or harmful arthropods (insects), and, consequently, these chemicals are usually harmful to nontarget arthropods (crustaceans). Pesticide use is changing in the United States in that less persistent, more specific chemicals are replacing more persistent organochlorines, such as DDT and its family. For purposes of this chapter, pesticides will be separated and discussed according to chemical structure, i.e., organochlorines, organophosphates and carbamates,

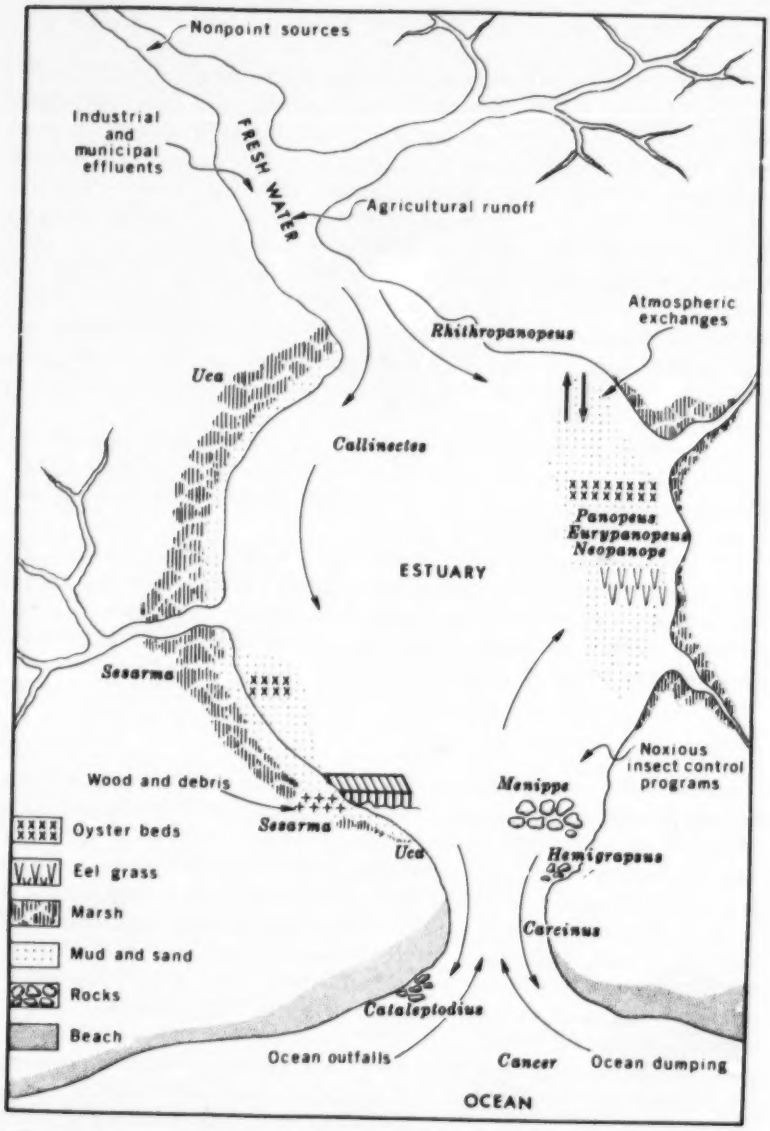

Fig. 1. Diagrammatic representation of an estuary showing generalized major habitats, sources of circulated materials, and relative position occupied by adults of brachyuran genera.

25

juvenile hormones, and insect growth regulators. The application of mirex to the coastal environment will be used as a case history because it illustrates the impact of a rather controversial pesticide on crabs and their environment.

1. Chlorinated Hydrocarbons

Chlorinated hydrocarbons, persistent pesticides that have been used in this country especially since the 1950s, include such compounds as DDT and its metabolites, dieldrin, mirex, and Kepone. These compounds generally are insoluble in water and much more soluble in lipids. Because of ubiquitous use in this country and persistence, these chemicals often appear as residues in marine organisms, including brachyuran crabs. For example, Albright *et al.* (1975) reported nondetectable to 22.0 ppb heptachlor epoxide and 23.0–295.8 ppb *p,p**-DDE in the tissue of *Cancer magister* from selected areas in the Georgia Straits near British Columbia. The sources of these chlorinated hydrocarbons were believed to be surface runoffs from aerial sprays, ground water, direct application for insect control, and domestic and industrial effluents. DDT and dieldrin residues from crabs and other organisms from San Antonio Bay, Texas, were reported by Petrocelli *et al.* (1974). Blue crabs, *Callinectes sapidus,* analyzed by a gas–liquid chromatograph with an electron capture detector, were found to contain rather high incidence of DDT, possibly caused by their ommnivorous or opportunistic feeding habits. Of 81 blue crabs analyzed, 94% contained DDT, 32% dieldrin, and 28% both chemicals. The amount of DDE ranged from nondetectable to 68.20 μg/kg or ppb DDE, and dieldrin ranged from nondetectable to 44.60 ppb. Modin (1969) examined residues of DDE, DDD, and DDT in Dungeness crab, *Cancer magister,* from the San Francisco region and found values of DDE from 40 to 62 ppb in stripped females and 54 to 430 ppb in ova. Commercial fishermen speculated that pesticide pollution might be a factor contributing to decline of the Dungeness fishery at San Francisco.

Biomagnification of dieldrin residues in blue crabs was studied by Petrocelli *et al.* (1975). Blue crabs, fed contaminated clam meat, concentrated dieldrin residues from 4.7 to 6.8 times the daily dose after 10 days of feeding. The authors warned that these animals were fed small amounts of food contaminated by dieldrin at relatively low levels over a short period of time. Under natural conditions in the field, animals consuming contaminated foods for several months or years may have a much higher concentration factor. In any event, it was clearly shown that dieldrin could move through a two-step food chain and be bioaccumulated by blue crabs.

Sheridan (1975) detected DDT and its metabolites in five out of six major organs in blue crabs collected from the York River in Virginia in 1972. Concentrations were highest in the hepatopancreas (55–217 ppb) but below the limit of detection in heart and serum. Variable residues also occurred in gonad samples (9–67 ppb), gill (6–31 ppb), and edible claw and back fin muscles (1–13 ppb).

DDT itself was not detected in any of the organs. Laboratory studies were conducted to determine the accumulation of DDT in the crab's organs and the transfer between organs, as well as the rate of metabolism and loss of DDT and its metabolites. Response to concentrations of 0.01, 0.1, and 1.0 ppm DDT varied among organs and suggested that DDT was transported from gills to the hepatopancreas via the blood stream. Since DDD concentrations were observed in gill and the hepatopancreas immediately after exposure to DDT, it was suggested that DDT is rapidly dechlorinated to DDD. The apparent site of DDT metabolism was the hepatopancreas. DDE concentrations in edible claw and back fin muscles increased with time after exposure to DDT.

Epifanio (1973) determined the uptake of another chlorinated hydrocarbon, dieldrin, by larvae of *Cataleptodius* (=*Leptodius*) *floridanus*. One group of larvae was exposed to 0.5 ppb in seawater and fed *Artemia salina* nauplii uncontaminated with dieldrin while another group reared in seawater and contaminated with dieldrin was fed nauplii contaminated with 213 ppb dieldrin. In the study, no distinction was made between dieldrin absorbed on the cuticle and dieldrin stored in other tissues. The larvae accumulated dieldrin 19.1 times as fast from 0.5 ppb in seawater as from 213 ppb in food; Epifanio thought that this rate of uptake can differentially affect the toxicity of dieldrin to crab larvae.

Other information developed in the laboratory has indicated that chlorinated hydrocarbons are extremely toxic to estuarine crabs. For example, Epifanio (1971) showed some effects of dieldrin on the development of two species of crabs, *C. floridanus* and *Panopeus herbstii*; 10 ppb in the water prohibited both species from completing their normal development, but the toxicity of dieldrin to *C. floridanus* larvae was more dependent on stage of development at exposure than length of exposure. Also, the effect of dieldrin on the molting process of that species was not as pronounced as the effect on survival. The author surmised that concentrations of 1 ppb dieldrin in seawater in the natural environment would change the larval population structure of these species of crabs. Juvenile *Callinectes sapidus* fed, molted, and grew for 9 months in seawater containing 0.25 ppb DDT but could survive only a few days in water containing in excess of 0.5 ppb (Lowe, 1965). Weis and Mantel (1976) determined the effects of chronic exposure to DDT on limb regeneration and molting in *Uca pugilator* and *Uca pugnax* after single limb and multiple autotomy. Autotomy of either one or seven limbs was induced by pinching the merus with scissors. The *R* value [(length of limb bud × 100)/carapace width] was used as an index for comparing crabs of different sizes. Results showed that DDT levels of approximately 10 ppb accelerated limb regeneration in fiddler crabs, particularly crabs stimulated to regenerate by multiple autotomy. Molting time was also shortened in these crabs by the presence of DDT. The stimulation of regeneration phenonoma, causing heightened excitation of the central nervous system, was suggested as an effect of DDT.

The recent tragedy at Hopewell, Virginia, where the chlorinated hydrocarbon, Kepone, was improperly handled and disposed, not only caused adverse human health effects but also had an impact upon aquatic organisms in the James River/Chesapeake Bay. Estuarine crabs were among the organisms most adversely affected. The Governor of Virginia recently closed fishing for male blue crabs, *Callinectes sapidus*, because of high residues of Kepone in their tissue and the prospect of Kepone reaching man through consumption of the organisms. Laboratory studies were conducted to determine the toxicity of Kepone to blue crabs and bioaccumulation of this chemical by the crabs under controlled laboratory conditions. Schimmel *et al.* (1979) conducted two long-term studies to determine toxicity, uptake, and distribution of Kepone in blue crabs. Kepone was administered to crabs in seawater (0.03 or 0.3 μg Kepone/liter of water) or fed in contaminated oyster meat containing 0.25 μg Kepone/gm meat. Uptake of Kepone in this instance was primarily through contaminated oysters. When crabs were held in Kepone-free seawater and fed Kepone-free oysters for 28 days, no loss of the insecticide was evident. Adverse effects were evident in crabs fed oysters that contained 0.25 μg Kepone/gm oyster. In separate experiments, crabs, fed Kepone-contaminated James River oysters that contained approximately 1.9 μg Kepone/gm oyster and then Kepone-free oysters for 90 days, still contained detectable concentrations of pesticide in tissues analyzed at the experiment's conclusion. Also, blue crabs that ate oysters containing Kepone in concentrations similar to those found in oysters from the James River died in greater numbers or molted less frequently than crabs fed Kepone-free oyster meat. Schimmel *et al.* suggest, from this data base, that Kepone may be a factor in the present decline in the James River crab fishery.

Two field studies demonstrating the effect of chlorinated hydrocarbons on fiddler crabs, *Uca pugnax*, are of particular interest (Krebs *et al.*, 1974). Test plots in a marsh near West Falmouth, Massachusetts, were prepared by adding weekly doses of a commercial fertilizer manufactured from sewage sludge. To one plot was added sewage containing 25.2 gm/m^2 (HF) and to the other 8.4 gm/m^2 (LF). Two untreated plots served as control. The first indication of an effect was observed in the fall, when a lower density of crabs began to overwinter in plots treated with the higher dose of sewage contamination. The number of crabs dead or inactive on the marsh surface increased in both treated plots as compared to controls. Residue analysis of *U. pugnax* samples showed low but fairly uniform amounts of DDE; these concentrations were about three times the level present in the sediment. Chemical analysis of the sediment also revealed aldrin and dieldrin. The residues of dieldrin in live crabs correlated well with the degree of locomotor impairment observed in the crabs, but aldrin was independent of impairment. Krebs *et al.* concluded that insecticide contaminants were responsible for drastic reduction in the test fiddler crab population.

The interaction of temperature and DDT residues on *C. sapidus* mortality was

studied by Koenig *et al.* (1976) in DDT-contaminated and uncontaminated salt marshes in the northern Gulf of Mexico. Residue samples in the crabs and sediment were analyzed on a Varian 2100 gas chromatograph with a tritium electron-capture detector. DDT in the contaminated marsh originated from a dog fly (*Stomoxys calcitrans*) control program in which certain areas were sprayed once or twice per year. The uncontaminated area was some distance away and residue analysis indicated that the inhabitants of the controlled area were virtually pesticide-free. It was observed that blue crab mortalities occurred in the DDT-contaminated population, whereas no mortalities were observed in uncontaminated blue crab populations when there was a simultaneous decrease in water temperature. The total amount of DDT in blue crabs from the contaminated marsh was variable but each amount was higher than residues from the uncontaminated control areas. Analysis of the tissue of the dead and dying crabs revealed DDT residue concentrations as high as 39.0 ppm in the hepatopancreas and 1.43 ppm in muscle tissue. Although this study did not indicate how reduced temperatures interact with body burden to produce the toxic symptoms, three mechanisms were suggested: (1) DDT residues are released from stored lipids during periods of reduced temperature; (2) low temperature favors the DDT–nerve membrane complex; and (3) acute effects could be amplified through impairment of behavioral characteristics of the crabs in low temperatures.

2. *Mirex and Crabs: A Case History*

The impact of mirex (a chlorinated organic pesticide used to control fire ants in the southeastern United States) on estuarine crabs is illustrative of the capacity of the crabs to accumulate chlorinated hydrocarbons and their sensitivity to these chemicals. Mirex was developed by Allied Chemical Company to replace dieldrin and heptachlor, two persistent chlorinated hydrocarbons that were formerly used to eradicate fire ants but were especially toxic to nontarget aquatic organisms. Mirex bait was prepared by adding mirex to soybean oil and sorbing the resultant mixture onto corn-cob grits. The bait was usually applied by aerial spraying. Unfortunately, mirex was not adequately tested prior to being dispersed throughout the coastal environment. For example, routine 48-hour bioassays did not reveal toxic properties of mirex to crabs and other estuarine crustaceans. After the mirex spraying program began, subsequent studies showed that crabs could accumulate mirex from the environment and that this accumulation could be toxic.

Several field studies showed bioaccumulation of mirex after application to coastal and other aquatic habitats. McKenzie (1970) detected mirex in 22 out of 50 crab samples examined from a coastal area in South Carolina. Residue levels varied from a low of 0.005 to 0.209 ppm. In a cooperative effort among the states of North Carolina, South Carolina, Georgia, and Florida, Mahood *et al.* (1970) examined 1950 blue crabs and found that 35% contained detectable levels of

mirex. Borthwick *et al.* (1974) conducted a field evaluation of the accumulation and movement of mirex in selected estuaries in South Carolina in conjunction with aerial application of the pesticide. The data revealed that some mirex was translocated from treated lands and high marsh to estuarine biota. Biological concentrations of mirex occurred especially in predators such as raccoons and birds; blue crabs collected in this study contained from 0 to 0.60 ppm of mirex. A follow-up study conducted 2 years after aerial application showed that the mirex level in animals had dropped considerably. Blue crabs collected at two freshwater stations in June, 1972, contained an average of 0.026 ppm. None of these field studies was designed to show the effect of mirex on crabs in the natural environment other than through visual observations of mortalities in the field during sampling.

Parallel studies conducted in the laboratory aided in determining the impact of mirex residues in nature. McKenzie (1970) and Lowe *et al.* (1971) studied the effects of mirex on estuarine organisms, including blue crabs and fiddler crabs. Independently, these investigators found that mirex exhibited a delayed toxicity to crabs. McKenzie found that adult and subadult (76–127-mm carapace width) blue crabs were not affected by doses 10 times the standard application rate of mirex. Juvenile blue crabs of less than 76 mm width were extremely sensitive to mirex bait and the toxicity was temperature dependent. Lowe *et al.* allowed juvenile blue crabs to eat one particle of mirex bait. Four weeks after the bait was fed to the crabs, whole-body residue analysis was conducted by electron-capture gas chromatography. Nineteen of 25 crabs exposed to the bait were paralyzed or dead at the end of the experiment; 92% contained residues of mirex. The residues in surviving crabs averaged 0.99 ppm. Fiddler crabs, *U. pugilator*, were exposed in a similar manner. The crabs readily picked up and ingested particles of the mirex bait; paralysis or death occurred within one to several weeks, depending on the amount of bait eaten and the temperature of the experimental environment. Residues of mirex in fiddler crabs averaged about 0.30 ppm.

The accumulation of mirex from water and its distribution in adult blue crabs were determined by Schoor (1974). Adult crabs were exposed from 15 minutes to 16 hours to mirex labeled with carbon-14. Mirex residues were found in the hepatopancreas, brain, thoracic ganglion, muscle, and hemolymph serum. Schoor suggested that mirex was absorbed through the gills because of the manner in which it appeared in the hemolymph and hepatopancreas. In experiments with juvenile blue crabs, Leffler (1975) studied the effect of ingested mirex and DDT. Mirex proved to be a much more potent stomach poison than DDT. Subacute levels of mirex (0.02 to 0.2 ppm) caused pronounced metabolic rate elevation. This elevation was observed at all test concentrations above the minimum level eliciting the response. The possibility that mirex and other chlorinated hydrocarbons could act synergistically to affect the capacity of juvenile blue crabs to obtain food and oxygen to accommodate both normal

growth and increased metabolism was discussed, suggesting that ingested mirex resulted in outright poisoning, metabolic rate elevation, decreased muscular coordination, and reduced carapace thickness/width ratio. It was concluded that this chemical is potentially disastrous with respect to blue crab populations.

The effects of mirex on development and survival of two other crabs in laboratory cultures, *Rhithropanopeus harrisii* and *Menippe mercenaria*, were differential in that an increase in duration of developmental stages with increasing concentrations appeared in *R. harrisii*, but no such effect was noted in *M. mercenaria* (Bookhout *et al.*, 1972). Conversely, survival was reduced in relation to increased concentrations in both species but *M. mercenaria* was much more sensitive than *R. harrisii*. Any extension of the duration of crab developmental stages could have ecological implications if crabs in various stages of development are subjected to adverse temperature, salinity, or other environmental conditions.

In experiments conducted at the community or systems level, simulated marsh systems were constructed with populations of various estuarine organisms, including crabs. Four 28-day seasonal experiments were conducted by Tagatz *et al.* (1975). To simulate movement of mirex bait from terrestrial to saltwater environments, mirex was leached from fire ant bait by fresh water mixed with salt water and added to communities of blue crabs, pink shrimp (*Penaeus duorarum*), grass shrimp (*Palaemonetes pugio*), and sheepshead minnows (*Cyprinodon variegatus*) at concentrations of 0.01–0.50 ppb. Leaching was greatest in summer and least in spring. Greatest mortality occurred in the summer experiments at the highest water temperature and concentrations of mirex. The least mortality occurred in spring at next to the lowest temperature and at the lowest concentration. The earliest deaths of organisms occurred in blue crabs after 6 days of exposure; small juvenile crabs were more sensitive to leached mirex than were large juveniles. Mirex did not appear to affect growth or frequency of molting in crabs. All exposed animals concentrated mirex; blue crabs concentrated the chemical 2300 times the amount in the water. Sand substrate contained mirex up to 770 times that in the water. In a similar experiment, mirex bait was added to simulated marsh systems containing marsh plants, oysters, blue crabs, fiddler crabs, and two species of cyprinodontids (Cripe and Livingston, 1977). Samples of water, bait, and animals were analyzed periodically; all animals concentrated mirex. Three photoproducts of mirex accumulated on the bait particles. Oysters and one species of fish, but not crabs, accumulated one of the photoproducts. Samples were analyzed with a Varian 2100 gas chromatograph with two tritium detectors. The rates of uptake of mirex from the water appeared very similar in blue crabs and fiddler crabs, but blue crabs took up a much greater quantity than fiddler crabs. This result was attributed to differences in lipid concentrations of the viscera and muscle tissues of the two species. The results of

these system studies indicated again that application of mirex bait to a marsh area could result in rapid accumulation in resident organisms.

As a result of information gained in laboratory and field studies, the aerial application of mirex was limited to within 12 miles of the coastline, and efforts were made to avoid applying mirex to areas near rivers, streams, and other aquatic environments. It is possible that if full-scale aerial application of mirex bait had been permitted and the material spread indiscriminately over marsh and estuarine areas, severe effects on crab populations could have occurred. It is important that monitoring continue to determine that mirex applied under more restricted conditions still does not reach unacceptable levels in coastal regions.

3. *Organophosphates and Carbamates*

The trend in pesticide production and usage in this country is moving away from organochlorine chemicals to "second generation" chemicals, such as organophosphates and carbamates. The latter are often preferred over organochlorines because they are generally less persistent in the environment and often are more specific for target organisms. Because of the chemical characteristics of organophosphates and carbamates, their residues are difficult to measure and interpret, and require different analytical approaches (enzyme activity versus chemical analysis) (Coppage and Duke, 1971). These chemicals, however, can be extremely toxic to nontarget organisms such as crabs.

Bookhout and Costlow (1976) studied the effect of malathion on the complete larval development of *Rhithropanopeus harrisii* and *Callinectes sapidus* from the time of hatching until the first crab stage. *Rhithropanopeus harrisii* suffered a reduction in survival of larvae in each increase of concentration of malathion from 0.011 to 0.02 ppm. These concentrations also lengthened duration of zoeal and megalopa development. Survival of blue crab larvae decreased in concentrations from 0.02 to 0.08 ppm, but duration of development lengthened.

Caldwell (1977) found the zoeal stages of the Dungeness crab, *Cancer magister*, to be most sensitive to malathion and carbofuran. The lowest concentration of each chemical affecting survival was malathion, 0.02 μg/liter and carbofuran, 0.05 μg/liter. Sublethal effects of these pesticides either were not observed or were only slightly below the reported values for survival.

Studies of the effects of sevin on this species showed similar results. For example, Buchanan *et al.* (1970) reported that early larval stages were more sensitive to sevin than juveniles and adults. At 1.0-mg/liter concentration, sevin did not affect egg hatching in seawater but prevented molting of prezoeae to zoeae. Molting was delayed at concentrations as low as 0.0001 mg/liter. Data also were accumulated on the movement of sevin through a simple food chain and the resulting effects of the bioaccumulation of the chemical.

Several pertinent experiments have been completed on the impact of these

chemicals on crabs maintained under field conditions. Tagatz *et al.* (1974) found no effect of malathion on caged blue crabs at an application of 57 gm/ha through a thermal fog and ultra-low-volume aerosal spray. Dursban, when applied manually at 0.05 lb/acre, had no effect on fiddler crabs, but the crabs accumulated a residue of 4.62 ppm (Marganian and Wall, 1972). However, when the same amount of Dursban was applied by duster, numerous fiddler crabs were killed. In experimental sites treated with Abate in New Jersey, populations of fiddler crabs decreased about 20% (Ward and Howes, 1974). The decrease was attributed either to direct toxicity of Abate leached from a 2% granular formation or to a behavioral effect—disappearance of the escape reaction to predators. The possibility of a behavioral effect was studied further (Ward *et al.*, 1976) by treating open marsh areas with Abate, then screening some affected fiddler crabs from predators while leaving others exposed. There was a significant reduction in the unprotected fiddler population, giving credence to the sublethal behavioral effect theory.

4. Juvenile Hormone Mimics or Analogs and Insect Growth Regulators

If organochlorine chemicals are considered first-generation pesticides, and the less persistent organophosphates and carbamates as the second generation, then juvenile hormone mimics or analogs and growth regulators can be characterized as third-generation pesticides. The mimics or analogs are used to slow or prevent metamorphosis, or to alter specific life stages of insects. Because of the phylogenetic relationship between insects and crustaceans, these products would be expected to affect crabs as well as insects adversely, and the growth regulators can interfere with cuticle formation. This was borne out in a study of the effect of two compounds, MON-0585 and methoprene, on the development of larvae of *Rhithropanopeus harrisii* and *Callinectes sapidus* (Costlow and Bookhout, 1977). MON-0585 concentrations of 1.0 and 0.1 ppm did not affect survival of the zoeae of *R. harrisii* at salinities of 20 and 35‰. However, when the salinity was reduced to 5‰ a concentration of 1.0 ppm resulted in total mortality within the zoeal stages; 10 ppm was lethal and no zoeae developed beyond the first stage in all three experimental salinities. The time required for development from hatching to the megalopa, megalopa to crab, and hatching to final metamorphosis of the crab was not affected by concentrations of either 1.0 or 0.1 ppm MON-0585 in experimental salinities in which development occurred. Megalopa of *C. sapidus* were killed in salinities of 20‰ and 35‰ containing 10 ppm MON-0585, and 1 ppm killed 60% regardless of salinity. Methoprene, at a concentration of 0.1 ppm and a temperature cycle of 20–25°C, reduced survival from 20 to 25% in all salinities tested. However, juvenile crab stages I, II, III, and IV did not show any effect when maintained in the same combinations (Costlow and Bookhout, 1977). An additional study by Costlow (1977) showed that 1.0 ppm methoprene

resulted in total mortality of larval stages of *R. harrisii*, usually within the first 2 days of hatching. Christiansen *et al.* (1977) showed a significant reduction in survival of zoeae of *R. harrisii* with increasing concentrations of hydroprene, and an increase in duration of zoeal stages as the concentration of hydroprene increased.

Other laboratory studies have used behavior as an indicator of sublethal effect of juvenile hormone mimics on larval crabs (Forward and Costlow, 1976). The effect of MON-0585 on linear swimming speeds and phototaxis of *R. harrisii* was observed under controlled conditions. Swimming speeds were varied under microscopic illumination light as larvae were subjected to various concentrations of the chemical. The larvae decreased in sensitivity throughout developmental stages I through IV; in stage I, 0.1 ppm caused a significant increase in swimming speed over control; the same effect was created by 0.5 ppm in stages II and III and by 1.0 ppm in stage IV. The magnitude for both positive and negative phototaxis responses was depressed when the larvae were exposed to the higher test concentrations of MON-0585. The measured behaviors of these larvae were affected by 0.1 ppm MON-0585; early zoeal stages were the most sensitive since both swimming and phototaxis were affected at this concentration in both acute and chronic tests. Since the behavior patterns used as criteria in these studies are necessary for survival of larvae, Forward and Costlow suggested that caution must be exercised when using MON-0585 in areas where the larval crabs are present.

The growth regulator Dimlin has been shown to have a significant effect on survival of *Rhithropanopeus harrisii* larvae at concentrations of 1 ppb in water (Christiansen *et al.*, 1979), the authors suggesting that Dimlin may interfere with cuticle formation in crab larvae. Costlow (1977) discussed the effect of Dimlin on the development of the stone crab, *Menippe mercenaria*, and the blue crab, *Callinectes sapidus*. *Menippe mercenaria* could not survive 0.5 ppb Dimlin but *C. sapidus* was slightly more tolerant. Data from these and other experiments indicate that levels of this chemical which are toxic to insects are also toxic to zoeal stages of crabs.

Most studies on toxic organics report on parent compounds. The ability of breakdown products emanating from many of these compounds to persist in the marine environment is not known. Therefore, effects of these degradation products are not known, particularly those related to juvenile hormones. We are especially lacking in this information (see Table II).

B. Thermal Effects

Thermal discharges or thermal pollution from power-producing plants located in coastal and near-coastal environments can have an adverse effect on benthic populations, such as estuarine crabs. Much "baseline information" is available

TABLE II

SUMMARY OF PESTICIDE EFFECTS ON SEVEN SPECIES OF BRACHYURAN CRABS

Reference	Compound	Organisms	Exposure	Bioaccumulation	Observed effect
McKenzie (1970)	Mirex	Blue crabs		Residue levels varied 0.0005–0.209 ppm	Detected mirex in 22 of 50 sampled
Mahood *et al.* (1970)	Mirex	Blue crabs			Examined 1950; 35% contained detectable levels of mirex
Borthwick *et al.* (1974)	Mirex	Blue crabs	Aerial spraying	0–0.60 ppm	Two-year follow-up study at two freshwater stations contained average of 0.26 ppm
McKenzie (1970)	Mirex	Blue/fiddler crabs			Adults and subadults were not affected by doses 10 times the standard application. Juveniles of less than 76 mm were extremely sensitive
Lowe *et al.* (1971)	Mirex	Juvenile blue crabs	Hot soybean oil with mirex on corncob grits. Each crab exposed to one particle of bait for 4 weeks. Whole body residue analysis made on each crab.		Nineteen of 25 exposed paralyzed or dead at experiment end; 92% contained residues of mirex
		Fiddler crabs	Same as for juvenile blue crabs		Paralysis or death occurred within 1 to several weeks, depending on amount eaten and temperature; mirex in residue about 0.30 ppm

35

Schoor (1974)	Mirex with ^{14}C	Blue crab	15 minutes to 16 hours		Residues found in hepatopancreas, brain, thorax ganglion, muscle and hemolymph serum
Leffler (1975)	Mirex/DDT	Juvenile blue crabs	0.02 to 2 ppm mirex	Mirex more potent stomach poison than DDT	Caused metabolic rate elevation. Elevation observed at all test concentrations. Suggest possibility of ingested mirex resulting in outright poisoning, decreased muscular coordination, and reduced carapace thickness-width ratio
Bookhout *et al.* (1972)	Mirex	*R. harrisii* and *Menippe mercenaria*	0.1 to 10 ppb zoeal stage; 0.01 to 0.1 ppb megalopal stage		Survival reduced in relation to increased concentration in both but *M. mercenaria* more sensitive that *R. harrisii*. Greater the concentration from 0.01 to 1.0 ppb, the larger percentage of extra 6th zoeal stages in *mercenaria* but not in *harrisii*.
Tagatz *et al.* (1975)	Mirex	Blue crabs, pink shrimp, grass shrimp, and sheepshead minnows	Less than 0.3 μg/liter mirex leached from fire ant bait by fresh water and mixed with salt water	Blue crabs concentrated mirex 2300 times amount in water. Sand substrate contained mirex up to 770 times that in water	

(*Continued*)

TABLE II (*Continued*)

Reference	Compound	Organisms	Exposure	Bioaccumulation	Observed effect
Cripe and Livingston (1977)	Mirex bait (0.3% mirex)	Blue crabs, oysters, and fiddler crabs	Analyzed on Varian 2100 gas chromatograph with 2 tritium detectors		Application of mirex to marsh could result in rapid accumulation in resident organisms
Albright *et al.* (1975)	Heptachlor epoxide	Dungeness crabs, *Cancer magister*	Sources believed to be surface runoffs from aerial sprays, ground water, direct application for insect control	22.0 ppb	
	Paraprime DDE	*C. magister*		23.0–295.8 ppb	
Petrocelli *et al.* (1974)	DDT; dieldrin	Blue crabs		81 analyzed: 94% contained DDT, 32% dieldrin, and 28% contained both	
Modin (1969)	DDE, DDD, DDT	Dungeness crabs		40–62 ppb in stripped females and 54–430 ppb in ova	
Petrocelli *et al.* (1975)	Dieldrin	Blue crabs	Fed small amounts of contaminated food at low levels over short period of time	Fed contaminated clam meat with dieldrin residues from 4.7–6.8 times daily doses after 10 days of feeding	Dieldrin could move through two-step food chain and be bioaccumulated by crabs
Sheridan (1975)	DDT	Blue crabs		Highest concentration in hepatopancreas (55–217 ppb) and below level of detection in heart and serum. Residues in gonad samples variable	DDT itself not detected in any of organisms

37

				(9–67 ppb). Residue levels low in gill (6–31 ppb) and edible claw and back fin muscles (1–13 ppb)	
Epifanio (1973)	Dieldrin	*Cataleptodius floridanus*	0.5 ppb in seawater and fed *Artemia salina* nauplii not contaminated with dieldrin; another group in seawater contaminated with dieldrin but fed nauplii contaminated with 213 ppb	Accumulated dieldrin 19.1 times as fast from 0.5 ppb in seawater as from 213 ppb in food	
Epifanio (1971)	Dieldrin	*Cataleptodius floridanus* and *Panopeus herbstii*	10 ppb		Prevented both species from completing normal development but toxicity to *C. floridanus* larvae more dependent on stage of development at exposure than length of exposure
Lowe (1965)	DDT	Juvenile blue crabs			0.25 ppb (molted and grew for 9 months); but survived only a few days with excess of 0.5 ppb
Weis and Mantel (1976)	DDT	*Uca pugilator; U. pugnax*	10 ppb accelerated limb regeneration in fiddler crabs		Autotomy of either one or seven limbs induced by pinching merus with scissors. Molting time shortened; heightened excitation of central nervous system

(*Continued*)

TABLE II (*Continued*)

Reference	Compound	Organisms	Exposure	Bioaccumulation	Observed effect
Schimmel *et al.* (1979)	Kepone	Blue crabs	0.03 or 0.3 μg/liter in seawater or in contaminated oyster meat containing 0.25 μg Kepone/gm meat	Uptake primarily through contaminated oysters	Crabs held in Kepone-free water and fed Kepone-free oysters for 28 days; no loss of insecticide evident. Adverse effects evident in crabs fed oyster with 0.25 μg/gm Kepone.
Krebs *et al.* (1974)	Chlorinated hydrocarbons	*Uca pugnax*	25.2 and 8.4 gm/m²		Lower density of crabs over winter in plots with higher dose of sewage contamination. Death increased in both plots. Low but uniform amounts of DDE; concentration three times level in sediment. Aldrin and dieldrin also present in sediment
Koenig *et al.* (1976)	DDT and temperature	Blue crabs	DDT in contaminated marsh originated from dog fly control program (area sprayed 1 or 2 years). Dead and dying revealed 39.0 ppm in hepatopancreas and 1.43 ppm in swimmeret muscle		Mortalities occurred at same time as decrease in water temperature

on the thermal limits of marine organisms (Kinne, 1964), and of crabs in particular (Tagatz, 1969), including field observations on the impact of thermal effluents on crab populations.

Detailed biochemical studies of the effect of thermal stress on serum glucose and protein levels in blue crabs have shown that thermal stress altered levels of serum glucose and that this alteration could be used as a physiological indicator of thermal stress (Lynch, 1974). Other serum constituents, such as total serum protein levels, were not affected by thermal stress. Lynch proposed an index of conditions for blue crabs based on serum glucose concentrations that could vary, depending on a particular situation, even when the cause of the stress is not known. Leffler (1972) studied some effects of temperature on the growth and metabolic rate of juvenile blue crabs in the laboratory. Growth, of course, was shown to be dependent upon temperature. Crabs maintained at temperatures of 34° and 27°C grew faster than those in temperatures of 13°, 15°, and 20°C. Mortality was directly proportional to temperature between 13° and 34°C and was very high during ecdysis at higher temperatures. Leffler suggested that crabs living in regions of heated discharge (because of their mobility) could extend their growing season without decreasing size by actively avoiding areas of higher temperatures. Additional studies in the laboratory conducted by Burton *et al.* (1976) exposed blue crabs and mud crabs to rapid 5°C increases above ambient. The experimental animals were maintained at that temperature for a specific time; then the temperature was allowed to return to ambient over another specified time. Burton *et al.* pointed out the loose use of the term "thermal stress" in the literature, and defined "thermal stress" for their experiments as a stimulus that produces a significant deviation from normal physiological whole-animal consumption(Q_{O_2} or weight specific oxygen consumption responses)—not as a stimulus that necessarily causes a sublethal or prelethal effect. No significant changes in the Q_{O_2} patterns for blue crabs and mud crabs were noted at any acclimation temperature tested as a result of thermal exposure. Mihursky *et al.* (1974) completed extensive work on temperature–salinity effects on osmoregulation in crabs. Among their results are indications that size, but not sex differences, affected osmoconcentration, and that smaller crabs showed greater tolerance to thermal stress at high salinities than did larger crabs.

Copeland and Davis (1972) studied the effect of temperature on blue crabs in ambient pool experiments and found a large increase in the volume of blue crabs per pool during a spring experiment, particularly in heating pools. In summer and winter experiments, the change in volume of blue crabs, or biomass, was less than that observed during the spring experiments. Sewage added to the pools did not affect mortality; crabs in pools receiving sewage were significantly larger than those receiving heat alone—an effect related to the additional food available to the crabs in pools receiving the sewage. Studies by Gallaway and Strawn (1975) on seasonal abundance and distribution of blue crabs in a Galveston Bay area receiving hot water discharge from a generating station provided evidence

that crabs avoided the hottest water except for feeding during hot months of the year. Abundance and distributional patterns in their samples indicated that the discharge in this area had no detrimental effect on the blue crab population.

C. Oil

Crabs as well as other estuarine organisms can be adversely affected by oil and and oil products. Oil can enter the estuarine environment through accidental spills, normal operations of oil tankers, offshore production, and disposal of oil waste material. In addition, some oil originates from atmospheric transport which includes hydrocarbons from combustion engines. Oil can affect crabs thrcugh direct toxicity, destruction of habitat, and damage to a fishery resource through tainted crab meat. Dolan *et al.* (1970) summarized these potential effects:

1. Low-boiling, saturated hydrocarbons can cause cell damage and death, especially in larval and juvenile stages of marine organisms.
2. Higher-boiling, saturated hydrocarbons occur naturally in some organisms but may interfere with chemical communication used by animals as they feed and reproduce.
3. Olefinic hydrocarbons, found in gasoline and other refined products, will combine with chlorine and other elements to produce toxic mixtures.
4. Aromatic hydrocarbons are probably the most acutely toxic to marine organisms other than petroleum fractions, including benzene, toluene, and phenols.
5. Higher boiling aromatics include benzpyrene and 1,2, benzanthracene which have been isolated from crude oil.
6. Nonhydrocarbons include nitrogen, oxygen, sulfur, and metal compounds.

Several field observations have confirmed that crabs can accumulate different fractions of oil and that the oil and oil products are toxic. For example, a relatively minor oil spill in West Falmouth, Massachusetts, released approximately 700 tons of No. 2 fuel oil into coastal waters. Blumer *et al.* (1970) reported the toxic effects of this spill on crabs and other marine organisms, showing that the coastal area has been slow to recover and that the extent of some damage has intensified with time.

Laboratory studies have shown the capacity of crabs to accumulate oil. *Callinectes spadius* accumulated paraffinic and aromatic hydrocarbons including benzopyrene, fluorene, napthalene, and other fractions (Lee *et al.*, 1976). When given radiolabeled hydrocarbons in food, the crabs assimilated 2–10% and excreted the remainder. Hydrocarbons, when taken up through water, were elimi-

nated chiefly through fecal material. The hepatopancreas accumulated most of the hydrocarbons; 20 days after exposure to labeled hydrocarbons, only the hepatopancreas contained radioactivity. The studies suggest that the hepatopancreas was the site of hydrocarbon metabolism; no evidence was presented to show the storage of hydrocarbon by any other tissues. Burns (1976) examined the fiddler crab, *Uca pugnax*, for its capacity to metabolize foreign hydrocarbons. It was determined, by using aldrin epoxidation rates in microsomes from various body tissues, that *Uca pugnax* has the microsomal mixed function oxidase system necessary to oxidize foreign hydrocarbons. Rates of oxidation were slow, compared to those for insecticides in freshwater invertebrates. Based on *in vivo* naphthalene oxidation rates, metabolism alone could not clear body tissues of foreign hydrocarbons within the life span of the crab. Burns suggested that even under ideal conditions this lack of biochemical ability to metabolize foreign hydrocarbons partially could account for sensitivity of the organism to this type of chemical pollution.

Other laboratory studies have been directed toward determining sublethal effects of oil and other petroleum products on crabs. Takahashi and Kittredge (1973) studied sublethal effects of crude oil and petroleum products containing water-soluble components and the effect of these components on chemoreceptors in marine organisms. Many species (including crabs) depend upon chemoreception to locate food and sexual partners. Obviously, adverse influences on these important life functions could cause effects that would not be revealed in normal toxicity studies. These investigators found that exposure of an intertidal crab, *Pachygrapus crassipes* (a grapsine whose general ecology was not outlined above), to the water-soluble extracts of two crude oils inhibited the feeding response and the mating stance of males when exposed to the female's sex pheromone. The inhibition was found to be persistent when the crude oil concentration of the water-soluble fraction was below 10^{-8} in concentration (assuming that 1% of the crude oil application was extracted into seawater). Further studies showed that monoaromatic hydrocarbons were effective as inhibitors of chemoreception for relatively short periods of time—30 minutes to 1 hour; however, polynuclear hydrocarbons (such as naphthalene and binaphthyl) inhibited the crabs for 8 to 11 days, anthracene for 13 days. Evidently, crabs are sensitive through chemoreception to a minute concentration of aromatic hydrocarbons in seawater.

Blue crabs have also been exposed under laboratory conditions to No. 2 fuel oil near Narragansett, Rhode Island. Melzian (1977) exposed adult male blue crabs to four concentrations of seawater containing 1, 5, 10, and 20 ppm of No. 2 fuel oil in a continuous flow-through bioassay system. The experiments were conducted from August to October. The LC_{50} for 96 hours for the No. 2 fuel oil was 14.1 ppm and the LC_{50} 7-day value, 10.5 ppm. Preliminary experiments showed that the acute toxicity of No. 2 fuel oil may vary seasonably in that

animals were more sensitive to 10 ppm No. 2 oil in seawater with a temperature of 20.0°C, than those exposed to the same concentration in seawater of 5.6°C. Preliminary electron microscopic studies of the antennules of a single crab that survived for 60 days in a 1-ppm exposure showed no differences from control animals. However, the aesthetascs (chemosensory hairs) of the dosed animal were infected with filamentous bacteria or fungi. The author suggested that this "infection" might have occurred because of a lowering of immunological resistance of exposed animals. These results are especially interesting with respect to the previously reported experiments of Takahashi and Kittredge.

Oil can taint or lower the palatability of crabs and other marine organisms. A panel of experts experienced in organoleptic tests for determining taste in marine organisms followed guidelines proposed by the American Society for Testing Materials to determine the effect of two crude oils that had previously been tested for LC_{50}'s with penaeid shrimp (Knieper and Culley, 1975). The panel's results showed a significant decrease in tainting taste with decreasing concentrations of the crude oil. Threshold values for each oil were 620 and 1250 ppm. The same lighter fractions of the crude oil that are most toxic to shrimp also may be the part of the crude oil that imparts an oily taste to crab meat. There were some indications in preliminary test trials that proximal portions of the appendages and the anterior muscles were more affected by the oil than distal appendages and posterior muscles.

D. Metals

Metals, among elements that normally occur in marine crabs, are required for physiological processes, but can become toxic in excess amounts. Unfortunately, crabs can accumulate excess or toxic quantities of metal from seawater containing metal contamination from industrial wastes and other sources. Much information is available on metal residues (particularly mercury and cadmium) found in crabs and the effects of these metals on their welfare.

Studies by Fowler *et al.* (1975) related the many tons of trace metals annually released in southern California coastal basins to tissue burdens of trace metals in bottom-dwelling marine species, including the crabs *Cancer anthonyi* Rathbun (parallels northern half of *C. magister* range) and *Mursia gaudichaudii* H. Milne Edwards (marine crab ranging from near San Francisco to central Chile). These analyses were performed by proton-induced X-ray emission analysis and by atomic absorption spectroscopy. X-Ray examination of muscle samples from *C. anthonyi* showed high levels of potassium and calcium followed in abundance by bromine, zinc, iron, arsenic, strontium, selenium, and other trace metals. Surprisingly, arsenic and selenium were in higher concentration in those samples collected from noncontaminated regions than those collected from contaminated regions. Atomic absorption data from *M. gaudichaudii* showed muscle concen-

tration similar to that found in the *C. anthonyi*. Considerable variation was found among concentrations of the various metals in tissues; not all samples contained all the metals. A wide variation in the concentration of the metals in tissues of the animals is not unexpected because of the migratory habits of these crabs and because of environmental factors such as transport of metals by the California currents. These findings indicate that muscle and viscera of bottom-dwelling marine organisms living in an area polluted by heavy metals reflect this pollution, although they did not show conclusively that the levels in the tissue were a reflection of levels in the bottom sediments.

A preliminary survey of mercury and other metals in tissues of two species of crabs from Fraser River mudflats, British Columbia, was conducted by Parsons *et al.* (1973), who separated the Fraser River mudflat community into two areas, Sturgeon Bank and Roberts Bank, and analyzed the mercury content in muscle of *Cancer magister* by a flameless cell on an atomic absorption spectrophotometer. On a dry-weight basis, crabs of similar carapace width from Sturgeon Bank contained more mercury than those from Roberts Bank. For example, for a carapace width of 147 mm, crabs from Sturgeon Bank contained 3.7 ppm mercury and those from Roberts Bank contained only 0.32 ppm. The Vancouver City sewer outfall empties into Sturgeon Bank and the differences in mercury content might be due to this source of metal pollution. The mercury content of younger crabs on Sturgeon Bank was much lower than the older ones, and this was attributed to feeding habits. Young crabs are much more specific in their food requirements while the older crabs have greater variety in their diet, including detritus.

Several species of crabs and other decapod crustaceans from Plymouth, England, were analyzed for zinc and copper content by Bryan (1968). The majority of values, obtained through dithizone method and atomic absorption spectrophotometry, ranged from 20 to 35 μg metal/gm tissue. Bryan attributed this rather narrow range to the fact that the concentrations of these metals are regulated in the body fluids. Zinc and copper distribution within the body of the crabs, as well as methods for excreting these metals, are discussed.

Many data are available describing the toxicity of various metals, particularly mercury and cadmium, to crabs. For example, Calabrese *et al.* (1977) reviewed the effects of cadmium, mercury, and silver on marine organisms, including crabs. These and other workers in the field stress the need for knowledge of sublethal effects in order to determine "true" toxicity. These effects include such criteria as changes in oxygen consumption, osmoregulation, regeneration, ecdysis, and behavior. Also, effects from changes in temperature and salinity regimes on a crab's response to metal stress are most important. The following publications were selected to indicate the "state of the art" in determining lethal and sublethal effects of metals on marine crabs.

4/4

Knowledge of the accumulation and loss of mercury by crabs is most useful in determining the toxic effects of this metal. Vernberg and O'Hara (1972) investigated the effects of various temperature and salinity regimes on the accumulation of mercury by the fiddler crab, *Uca pugilator*. Although the total mercury content of gill and hepatopancreas remained essentially the same, the amount of the metal in each tissue varied under the different environmental conditions. Some insight into the mechanisms of mercury toxicity in crabs was noted, as the efficiency in the transport of mercury from gills to hepatopancreas increased with higher temperature. This might explain the toxicity of mercury to crabs at low temperature, as determined in another experiment by Vernberg and Vernberg (1972).

The biological half-life of inorganic mercury in *Cancer magister* was studied by Sloan *et al.* (1974). Inorganic mercury was added to seawater in the form of mercuric nitrate in a dosing aquarium. Crabs were removed after a specified time, placed in unpolluted seawater, and then analyzed at various time intervals. Mercury content was determined with an atomic absorption spectrophotometer containing a cold vapor apparatus. Analyses of data indicated a 25-day half-life of mercury under these experimental conditions. Three theoretical models were tested by computer program and the results caused the authors to question the validity of the use of the negative exponential "biological half-life." It would be interesting to compare the biological half-life of mercury taken up through food, as opposed to water only.

In study of the effect of mercury on larval *Uca pugilator* (DeCoursey and Vernberg, 1972), larvae were exposed to mercuric chloride in seawater at test concentrations of 180, 1.8, and 0.018 ppb. Analyses of mercury were accomplished with an atomic absorption spectrophotometer. Larval stages were significantly affected at 180 ppb of mercuric chloride within 24 hours, and the other test concentrations had deleterious effects but did not kill the larvae. Although these larvae were able to survive, attrition rate was greatly accelerated when compared to controls. It was also noted that sensitivity was related to developmental stage. Adult crabs can survive 180 ppb at ideal conditions of temperature and salinity for several hours, but stage V larvae survived only 6 hours, while stage I survived 24 hours. DeCoursey and Vernberg suggested that larvae would be even more susceptible to mercury in the environment where they would be subjected to additional temperature and salinity stresses.

Adult *Uca pugilator* exposed under laboratory conditions similar to those used with the larvae showed much less sensitivity to mercury than larvae (Vernberg and Vernberg, 1972). Crabs were exposed to 0.18 ppm of mercuric chloride, under optimum conditions of 25°C and 30‰ salinity, to determine direct toxicity. These conditions were varied to determine possible synergistic effects among mercury, temperature, and salinity. Mercury was analyzed by a Mercury

Analyzer System-50. Adult crabs accumulated mercury from the water rapidly in gill tissue in lesser amounts than in hepatopancreas and green gland tissues. Preliminary studies showed that the adult crabs could survive in 0.18 ppm mercury for at least 2 months under optimum conditions but temperature and salinity stress shortened this time considerably. The crabs withstood low temperature and high temperature better than low salinity coupled with low temperature. It appeared that mercury adversely affected the metabolic rate of males more than females.

The sublethal effect of mercury and cadmium on *Uca pugilator* under stress from temperature and salinity (Vernberg and DeCoursey, 1977) has been analyzed in terms of survival, tissue uptake, metabolism, behavior, microscopic anatomy, and enzymatic activity. The crabs were exposed to mercuric chloride at concentrations of 180, 1.8, and 0.018 ppb, and cadmium chloride at various concentrations. Mercury content in water and animals was determined with an Atomic Absorption Spectrophotometer Model 303, Mercury Analyzer System 50, or Coleman Mass Spec 30. Radioactive cadmium was detected by scintillation. Mercury was more toxic to males than females and, as reported previously, both sexes were found to withstand mercury in combination with high temperature and low salinity better than low temperature and low salinity. However, cadmium was most toxic at high temperature and low salinities. Fifty percent of the males exposed to 180 ppb mercury died within 5 days, and those exposed to 4000 ppb cadmium died within 6 days. The mode of action of both cadmium and mercury was probably related to bioaccumulation on the gills with subsequent breakdown of osmoregulatory or respiratory functions. The greater sensitivity of males to the effects of mercury was not explained in this study, but it was suggested that differences in metabolic rates of the sexes could be a contributing factor.

In crabs exposed to a mixture of mercury (180 ppb) and cadmium (1000 ppb) for 72 hours, the uptake of mercury was more influenced by the presence of cadmium than cadmium by mercury, in gill tissue, and a lesser amount in hepatopancreas tissue. Cadmium appeared to eliminate or severely slow the transport of mercury from gills to the hepatopancreas.

Metabolic rates established for adult male and female crabs were essentially the same. After sublethal levels of mercury were added, the metabolic rate of crabs was decreased, and the rate for males was significantly lower than for females after 2 days of exposure. Cadmium quickly altered the compensatory metabolic temperature response. This mechanism is, of course, necessary for crabs to adjust to environmental factors in the natural environment.

The effects of mercury on the response of crab larvae to light showed that stage 1 larvae were strongly photopositive regardless of temperature or salinity, and their phototactic response was not altered at mercury levels of 1.8 ppb. The

TABLE III

SUMMARY OF METAL EFFECTS ON ESTUARINE BRACHYURAN CRABS

Reference	Metal	Organisms	Exposure	Bioaccumulation	Observed effect
Fowler *et al.* (1975)	Trace metals	*Cancer anthonyi*	Environmental	High levels of K, Zn, Fe, As, Sr, Se, and others	
Parsons *et al.* (1973)	Hg	*Cancer magister*	Environmental	0.32–3.7 ppm	
Bryan (1968)	Zn and Cu	Crabs and other decapod crustaceans	Environmental	20–35 μg/gm	
Calabrese *et al.* (1977)	Cd, Hg, and Ag	Marine, including crabs			
Vernberg and O'Hara (1972)	Hg	*Uca pugilator*	0.18 ppm Hg^{2+} 24, 48, and 72 hours, various temperature-salinity regimes		Improved efficiency in transport of Hg from gills to hepatopancreas with higher temp
Sloan *et al.* (1974)	Hg	*Cancer magister*	$Hg(NO_3)_2 \cdot H_2O$ added to dosing aquaria		25-day half-life of Hg
DeCoursey and Vernberg (1972)	Hg	*Uca pugilator*	$HgCl_2$ in seawater; test concentrations of 180, 1.8, and 0.018 ppb		Within 24 hours larvae significantly affected by 180 ppb; sensitivity related to development stage
Vernberg and Vernberg (1972)	Hg	*Uca pugilator*	0.18 ppm of $HgCl_2$ under 25°C and 30‰ salinity	Rapid in gill tissue, less in hepatopancreas and green gland	Adult crab can survive in 0.18 ppm Hg for 2 months with optimum conditions

Vernberg and DeCoursey (1977)	Hg, Cd	*Uca pugilator*	$HgCl_2$: 180, 1.8, 0.018 ppb. $CdCl_2$, various concentrations	Gills, with breakdown of osmoregulatory or regulatory functions	50% males exposed to 180 ppb of Hg died within 5 days; those exposed to 4000 ppb Cd died within 6 days
			Mixture of 180 ppb Hg and 1000 ppb Cd for 72 hours		Greater amount of Hg in gills, much less in hepatopancreas
Eisler (1971)	Cd	*Carcinus maenas*	$CdCl_2$: 20°C, 20‰, 96 hours		LC_{50} = 4.1 ppm
Collier *et al.* (1973)	Cd	*Eurypanopeus depressus*	$CdCl_2$: 25‰, 21°C, 1-12 ppm		LC_{50} = 4.9 ppm O_2 consumption varied greatly among individuals. No variance in O_2 consumption in different test concentrations
Thurberg *et al.* (1973)	Cd, Cu	*Cancer irroratus* *Cancer maenas*	$CdCl_2$ $CuCl_2 \cdot H_2O$ Various increasing concentrations, 48 hours		Mortality >1 ppm Cd Mortality >5 ppm Cu Survived 8 ppm Cd Survived 40 ppm Cu
Hutcheson (1974)	Cd	*Callinectes sapidus*	Cd: 11.14 ppm, 0.11 ppm, 0.0001 ppm	Gill, hepatopancreas, carapace	
O'Hara (1973)	Cd	*Uca pugilator*	96 hours at 10‰ and 30°C		LC_{50} = 6.8 ppm exposure lethal

response in stage III larvae, however, was reduced by this concentration of mercury.

This study showed that under optimum temperature and salinity regimes, adult fiddler crabs can tolerate higher levels of mercury and cadmium than are tolerable when these factors are at stress levels. Also, larvae were more sensitive to these heavy metals than adults and, therefore, provided a much more sensitive indicator of effects.

Other information is available on lethality and physiological responses of crabs to cadmium. Eisler (1971) exposed various marine species, including *Carcinus maenas* (the green crab), to cadmium chloride in acute static tests. Crabs were found to be less sensitive than the sand shrimp, *Crangon septemspinosa*, and more sensitive than the blue mussel, *Mytilus edulis*. The 96-hour lethal concentration for 50% of the test crabs was 4.1 ppm. A similar lethal concentration value for 72-hour, 4.9 ppm, was determined by Collier *et al.* (1973) for the mud crab, *Eurypanopeus depressus*. These investigators also studied oxygen metabolism of whole animals and gill tissues alone. The oxygen consumption in whole animals varied greatly among individuals, and there were no differences in overall oxygen consumption among various test concentrations. Consumption in gill tissue alone decreased as cadmium concentrations increased. In green crabs, *Carcinus maenas*, and rock crabs, *Cancer irroratus*, exposed to cadmium chloride in seawater (Thurberg *et al.*, 1973), cadmium depressed gill-tissue consumption in both species and elevated the blood-serum osmolality of green crabs. Interestingly, green crabs survived 8 ppm cadmium, whereas mortality of rock crabs occurred above 1.0 ppm. Tests with copper showed a graded loss of osmoregulation in both species exposed to increasing concentration of copper (most pronounced at lower salinities).

The influence of temperature and salinity on the uptake of cadmium in *Callinectes sapidus* and *Uca pugilator* has been studied in addition to toxicity to fiddler crabs. Hutcheson (1974) found gills and hepatopancreas to be the major sites of accumulation of cadmium in blue crabs, independent of the concentration in water. Accumulation of cadmium in the carapace reached an apparent equilibrium with amounts in the water, probably because of saturation of available sites. At 10 ppm cadmium in the water, crabs accumulate cadmium more rapidly at lower salinities. At these low salinities, rate of uptake is proportional to temperature. At lower concentrations of cadmium in water (0.11 and 0.20 ppm), the metal was not taken up over background levels in the claw. This is important in that cadmium would not be transported to man from the hardshell crab, because the claw makes up a great part of crab meat eaten by man. Similar results were obtained by O'Hara (1973) for the fiddler crab. The same temperature and salinity regime resulted in maximum toxicity of cadmium to fiddler crabs. A concentration of 6.8 ppm cadmium was lethal to 50% of the test population in 96 hours at 10‰ salinity and 30°C (see Table III).

E. Radionuclides

Radionuclides can enter the marine environment through effluents from nuclear reactors, fallout from nuclear testing, and numerous minor sources. At present, relatively little radioactivity enters the marine environment, but it is a potential source of pollution as the nation's energy requirements and the number of nuclear reactors increase. Radionuclides reaching the marine environment can remain in the water, precipitate, and become part of the sediments, or can be accumulated and transported by plants and animals.

Various monitoring studies have shown that crabs can accumulate and retain radioactivity from their environment. Tarchevskii and Skolova (1971) measured the strontium-90 content of some Black Sea organisms, including the shore crab, *Carcinus maenas*. Although the amount of strontium-90 increased from 1965 through 1968 and could be represented by the mathematical expression $C = 171.8 + 3.9t$, the rate of increase during this time was less than the rate of increase of other Black Sea organisms recorded from 1961 to 1965. Among the various radionuclides in Dungeness crabs from the Columbia River reported by Toombs (1965), zinc-65 was readily detected and averaged about 15 pCi/gm. This average would require a person to eat in excess of 1000 lb of crabs per year to exceed the recommended permissible intake rate of 8×10^6 pCi/year. A later survey showing seasonal distribution of zinc-65, manganese-54, and chromium-51 in Dungeness crabs was conducted by Tennant and Forster (1969). It is difficult to compare their results with those of Toombs because of differences in methods used to determine radioactivity in tissues (ashed versus wet tissue analysis). However, the 1969 survey showed a positive correlation between specific activity (amount of zinc-65) and the amount of stable zinc and river discharge. Most of the radioactivity in the soft tissue was from zinc-65, chromium-51, and manganese-54. Observations of specific activity of the three nuclides gave some insight into rates of turnover and environmental "reservoirs" for the metals.

The capacity of mud crabs, *Panopeus herbstii*, as part of an estuarine community to accumulate zinc-65 under various salinities, pH's, temperatures, and concentrations of zinc in the water was studied by Duke *et al.* (1967) in several 15-day experiments. All factors, except the total concentration of zinc, significantly affected accumulation of zinc-65, clarifying, to some extent, differences in accumulation of this nuclide by crabs in the field. These laboratory and field data, however, do not directly address the question of the effect of radioactivity on the crabs.

Little attention has been devoted to the effects of accumulated radiation on crabs, although the effects of gamma radiation from external sources have been studied in some detail. The fiddler crab, *Uca pugnax*, was subjected to graded doses of cobalt-60 radiation by Rees (1962). The lethal dose for 50% of the

exposed population over 30 days was 8209 rads. This value is two to three times higher than values for the grass shrimp, *Palaemonetes pugio*, irradiated in a companion experiment (Rees, 1962). Although the study was not specifically designed to determine sublethal effects, it was noted that molting did not occur in crabs that received dosages of 9750 rads and above, but occurred in crabs receiving 4785 rads and below.

The radiation sensitivity of three species of fiddler crabs, *Uca pugilator*, *U. pugnax*, and *U. minax*, was determined by Engel (1973). Each of the three species of crabs was irradiated with cobalt-60 and maintained under the same experimental conditions. When mean survival times were calculated at 60 days for the three species of crabs, *U. pugilator* and *U. minax* showed a dose-dependent pattern of survival time, i.e., decreasing survival with increasing dose. The relation was not as clear with *U. pugnax* because mean survival time was independent of dose above 4000 rads. Several explanations were discussed for different survival time for each of the species over the 60-day test period. The size of the organisms, salinity tolerance, and oxygen consumption rate all were rejected as possible explanations. Observed interspecific differences in the radiation sensitivities of crustaceans are not due to simple physiological or phylogenic relationships, but may be the result of complex interactions between the organism and its environment. Also, it is difficult to compare data on the effect of ionizing radiations on the survival of marine species because of the potential for environmental factors (such as temperature and salinity) to interact with radiation to alter expression of a particular effect.

Experiments concerned with interactions of radiation, salinity, and temperature on blue crab were conducted by Engel *et al.* (1973). This animal must osmoregulate to survive in the estuarine environment; it is possible that interactions of salinity, temperature, and radiation may have deleterious effects on the osmoregulatory control. Ionic composition and free amino acid level of hemolymph in the crabs were significantly affected by salinity and temperature, and radiation also interacted significantly with these factors to further alter the regulatory pattern. Radiation interacted with salinity and temperature, causing alteration in ionic regulation after irradiation.

In an investigation of the effects of radiation of juvenile blue crabs, *Callinectes sapidus*, Engel (1967) exposed the crabs to single and continuous doses of γ irradiation. For those given single doses the LC_{50} (30) was 51,000 rads. Definite behavioral effects were noted after the single exposures. For example, the crabs quit eating and became less antagonistic. Later, the crabs became sluggish and uncoordinated and eventually died. A neurological disorder was noted that was dose dependent. The crabs that were exposed continuously to irradiation had reduced survival and growth only at the dose rate of 29.0 rad/hour. Continuous exposure apparently caused death of the crabs through unsuccessful molting. At the lowest dose rate of 3.2 rads/hour, the growth rate of the crabs was greater than

the other irradiated groups or the controls. This enhancement of growth may have been actually an acceleration of the aging process.

The understanding of the radiation biology of marine decapod crustaceans, and in particular the crabs, is incomplete. Recent data indicate that some crustaceans may be as sensitive to acute doses of radiation as mammals (Engel, in press), and that the primary reason for the extremely high LD_{50}'s is that sufficient time was not allowed in past investigations for damage to fully manifest itself. Thus, possibly, it would be inappropriate to assume that all crabs have sensitivities (LD_{50}) in the kilorad range.

V. Conclusions

Research suggests that estuarine crabs are sensitive to many forms of man-made pollution, either being acutely affected or serving as indicators through sublethal effects. We have discussed effects of only a few major pollutants on crabs, and have not cited other important hazards such as alterations of the habitat resulting from dredging, channelization, the addition of large amounts of fresh water, and other industrial activities. The animals and their habitats will continue to receive pollution stress in the future, but efforts are being made to counteract these stresses. Recent information on the number of chemical compounds or entities indicates that about 63,000 chemicals are in common use (Maugh, 1978). Undoubtedly, some of these will find or have found their way into the natural environment and the habitat of estuarine brachyurans. As our quest for energy sources heightens, the probability increases for spills and exposure of marine crabs to oil and its components. Also, as the world requirement for food increases, the use of pesticides will probably increase, at least in the immediate future.

Conversely, recent evidence indicates that programs to improve water quality have gained momentum. New federal legislation to control the testing and release of toxic substances (Toxic Substance Control Act of 1977) is now in effect. The data base concerned with the effect of pollutants on crabs has increased in volume and in quality during the past few years. There is no reason to believe that this trend will not continue in the future.

Because of the importance of crabs in the coastal zone and the sensitivity of these animals to many pollutants, crabs will probably be used more in future water quality studies as "indicator species." Because of their sensitivity to many pollutants, crabs can often be used to predict adverse influences on the environment and to highlight the impact of these substances on themselves.

In summary, many forces acting to impact the coastal environment adversely are offset by other factors that offer some hope for maintenance and improvement. The authors view this improvement with cautious optimism.

Acknowledgments

We thank Jackie Holley for assistance in preparing the pollution ecology section, B. B. Collette and M. E. Tagatz for critical reading of the manuscript, Maria Diéguez for drafting the illustration, and Virginia Tucker for final typing. A number of colleagues have also aided with critical suggestions and references.

References

Abele, L. G. (1972). A reevaluation of the *Neopanope texana-sayi* complex with notes on *N. packardii* (Crustacea: Decapoda: Xanthidae) in the northwestern Atlantic. *Chesapeake Sci.* **13,** 263–271.

Abele, L. G. (1973). Taxonomy, distribution and ecology of the genus *Sesarma* (Crustacea, Decapoda, Grapsidae) in eastern North America, with special reference to Florida. *Am. Midl. Nat.* **90,** 375–386.

Ahsanullah, M., and Newell, R. C. (1977). The effects of humidity and temperature on water loss in *Carcinus maenas* (L.) and *Portunus marmoreus* (Leach). *Comp. Biochem. Physiol. A* **56,** 593–601.

Albright, L. J., Northcote, T. G., Oloffs, P. C., and Szeto, S. Y. (1975). Chlorinated hydrocarbon residues in fish, crabs, and shellfish of the lower Fraser River, its estuary, and selected locations in Georgia Strait, British Columbia—1972–73. *Pestic. Monit. J.* **9,** 134–140.

Allen, E. A., and Curran, H. A. (1974). Biogenic sedimentary structures produced by crabs in lagoon margin and salt marsh environments near Beaufort, North Carolina. *J. Sediment. Petrol.* **44,** 538–548.

Barnwell, F. H. (1968). The role of rhythmic systems in the adaptation of fiddler crabs to the intertidal zone. *Am. Zool.* **8,** 569–583.

Beers, J. R. (1958). An histological and histochemical study of the green gland of *Cancer borealis*. *Anat. Rec.* **131,** 531–532.

Bell, T. I., and FitzGibbon, D. S., eds. (1977). "Fishery Statistics of the United States, 1974," Stat. Dig. No. 68. Natl. Oceanic Atmo. Adm., Natl. Mar. Fish. Serv., U. S. Dept. of Commerce, Washington, D.C.

Blumer, M., Souza, G., and Sass, J. (1970). Hydrocarbon pollution of edible shellfish by an oil spill. *Mar. Biol.* **5,** 195–202.

Bookhout, C. G., and Costlow, J. D., Jr. (1976). Effects of mirex, methoxychlor, and malathion on development of crabs. *U.S. Environ. Prot. Agency, Off. Res. Dev.* [*Rep.*] *EPA* **EPA-600/3-76-007,** 1–85.

Bookhout, C. G., Wilson, A. J., Jr., Duke, T. W., and Lowe, J. I. (1972). Effects of mirex on the larval development of two crabs. *Water, Air, Soil Pollut.* **1,** 165–180.

Boolootian, R. A., Giese, A. C., Farmanfarmaian, A., and Tucker, J. (1959). Reproductive cycles of five west coast crabs. *Physiol. Zool.* **32,** 213–220.

Borthwick, P. W., Cook, G. H., and Patrick, J. M., Jr. (1974). Mirex residues in selected estuaries of South Carolina, USA, June 1972. *Pestic. Monit. J.* **7,** 144–145.

Bousfield, E. L. (1955). Ecological control of the occurrence of barnacles in the Miramichi estuary. *Natl. Mus. Can., Bull.* **137,** 1–69.

Bousfield, E. L., and Laubitz, D. R. (1972). Station lists and new distributional records of littoral marine invertebrates of the Canadian Atlantic and New England regions. *Natl. Mus. Nat. Sci. Publ. Biol. Oceanogr.* No. 5, pp. 1–51.

Broad, A. C. (1957). The relationship between diet and larval development of *Palaemonetes*. *Biol. Bull. (Woods Hole, Mass.)* **112,** 162–170.

Broekhuysen, G. J., Jr. (1936). On development, growth and distribution of *Carcinides maenas* (L.). *Arch. Neerl. Zool.* **2,** 257–399.

Bryan, G. W. (1968). Concentration of zinc and copper in the decapod crustaceans. *J. Mar. Biol. Assoc. U. K.* **48,** 303–321.

Buchanan, D. V., and Millemann, R. E. (1969). The prezoeal stage of the Dungeness crab, *Cancer magister,* Dana. *Biol. Bull. (Woods Hole, Mass.)* **137,** 250–255.

Buchanan, D. V., Millemann, R. E., and Stewart, N. E. (1970). Effects of the insecticide sevin on various stages of the Dungeness crab, *Cancer magister. J. Fish. Res. Board Can.* **27,** 93–104.

Burns, K. A. (1976). Hydrocarbon metabolism in the intertidal fiddler crab *Uca pugnax. Mar. Biol.* **36,** 5–11.

Burton, D. T., Richardson, L. B., Margrey, S. L., and Abell, P. R. (1976). Effects of low ΔT powerplant temperatures on estuarine invertebrates. *J. Water Pollut. Control Fed.* **48,** 2259–2272.

Butler, T. H. (1960). Maturity and breeding of the Pacific edible crab, *Cancer magister* Dana. *J. Fish. Res. Board Can.* **17,** 641–646.

Butler, T. H. (1961). Growth and age determination of the Pacific edible crab *Cancer magister* Dana. *J. Fish. Res. Board Can.* **18,** 873–891.

Caddy, J. F. (1973). Underwater observations on tracks of dredges and trawls and some effects of dredging on a scallop ground. *J. Fish. Res. Board Can.* **3,** 173–180.

Calabrese, A. F., Thurberg, P., and Gould, E. (1977). Effects of cadmium, mercury, and silver on marine animals. *Mar. Fish. Rev.* **39,** 5–11.

Caldwell, R. S. (1977). Biological effects of pesticides on the Dungeness crab. *U.S. Environ. Prot. Agency, Tech. Rep.* **68-01-0188,** 1–180.

Capen, R. L. (1972). Studies of water uptake in the euryhaline crab, *Rhithropanopeus harrisi. J. Exp. Zool.* **182,** 307–319.

Carpenter, J. H., and Cargo, D. G. (1957). Oxygen requirement and mortality of the blue crab in the Chesapeake Bay. *Chesapeake Bay Inst. Johns Hopkins Univ., Tech. Rep.* No. **13,** pp. 1–22.

Chamberlain, N. A. (1957). Larval development of *Neopanope texana sayi. Biol. Bull. (Woods Hole, Mass.)* **113,** 338.

Chamberlain, N. A. (1961). Studies on the larval development of *Neopanope texana sayi* (Smith) and other crabs of the family Xanthidae (Brachyura). *Chesapeake Bay Inst., Johns Hopkins Univ., Tech. Rep.* No. 22, pp. 1–35.

Chamberlain, N. A. (1962). Ecological studies of the larval development of *Rhithropanopeus harrisii* (Xanthidae, Brachyura). *Chesapeake Bay Inst., Johns Hopkins Univ., Tech. Rep.* No. 28, pp. 1–47.

Cheung, T. S. (1966). An observed act of copulation in the shore crab, *Carcinus maenas* (L.). *Crustaceana (Leiden)* **11,** 107–108.

Cheung, T. S. (1968). Trans-molt retention of sperm in the female stone crab, *Menippe mercenaria* (Say). *Crustaceana (Leiden)* **15,** 117–120.

Cheung, T. S. (1969). The environmental and hormonal control of growth and reproduction in the adult female stone crab, *Menippe mercenaria* (Say). *Biol. Bull. (Woods Hole, Mass.)* **136,** 327–346.

Christiansen, M. E. (1969). Crustacea Decapoda Brachyura. "Marine Invertebrates of Scandinavia," No. 2. Universitetsforlaget, Oslo.

Christiansen, M. E., and Costlow, J. D., Jr. (1975). The effect of salinity and cyclic temperature on larval development of the mud-crab *Rhithropanopeus harrisii* (Brachyura: Xanthidae) reared in the laboratory. *Mar. Biol.* **32,** 215–221.

Christiansen, M. E., Costlow, J. D., Jr., and Monroe, R. J. (1977). Effects of the juvenile hormone mimic ZR-512 (Altozar ®) on larval development of the mud-crab *Rhithropanopeus harrisii* at various cyclic temperatures. *Mar. Biol.* **39,** 281–288.

54

Christiansen, M. E., Costlow, J. D., Jr., and Monroe, R. J. (1978). Effects of the insect growth regulator Dimlin® (TH 6040) on larval development of two estuarine crabs. *Mar. Biol.* **50,** 29–36.

Christy, J. H. (1978). Adaptive significance of reproductive cycles in the fiddler crab *Uca pugilator:* A hypothesis. *Science* **199,** 453–455.

Churchill, E. P., Jr. (1919). Life history of the blue crab. *Bull. U.S. Bur. Fish.* **36,** 95–128.

Clay, E. (1965). "Literature Survey of the Common Fauna of Estuaries. 16. *Carcinus maenas* L." *Imperial Chemical Industries, Ltd. Brixham Laboratory,* PVM45/A/916. Brixham Lab., Imp. Chem. Ind. Ltd.

Collier, R. S., Miller, J. E., Dawson, M. A., and Thurberg, F. P. (1973). Physiological response of the mud crab *Eurypanopeus depressus* to cadmium. *Bull. Environ. Contam. Toxicol.* **10,** 378–382.

Connolly, C. J. (1925). The larval stages and megalops of *Rhithropanopeus harrisii* (Gould). *Contrib. Can. Biol.* [N. S.] **2,** 327–333.

Copeland, B. J., and Davis, H. L. (1972). "Estuarine Ecosystems and High Temperatures." Water Resour. Res., Inc., Raleigh, North Carolina.

Coppage, D. L., and Duke, T. W. (1971). Effects of pesticides in estuaries along the Gulf and southeast Atlantic coasts. *In* "Proceedings of the 2nd Gulf Coast Conference on Mosquito Suppression and Wildlife Management, held in conjunction with annual meetings of Louisiana Mosquito Control Association and Gulf States Council on Wildlife Fisheries and Mosquito Control, New Orleans, La., October 20–22, 1971," pp. 24–31.

Cornick, J. W., and Stewart, J. E. (1968). Pathogenicity of *Gaffkya homari* for the crab *Cancer irroratus. J. Fish. Res. Board Can.* **25,** 795–799.

Costlow, J. D., Jr. (1965). Variability in larval stages of the blue crab, *Callinectes sapidus. Biol. Bull. (Woods Hole, Mass.)* **128,** 58–66.

Costlow, J. D., Jr. (1967). The effect of salinity and temperature on survival and metamorphosis of megalops of the blue crab *Callinectes sapidus. Helgol. Wiss. Meeresunter.* **15,** 84–97.

Costlow, J. D., Jr. (1977). The effect of juvenile hormone mimics on development of the mud crab, *Rhithropanopeus harrisii* (Gould). *In* "Physiological Responses of Marine Biota to Pollutants" (F. J. Vernberg *et al.*, eds.), pp. 439–457. Academic Press, New York.

Costlow, J. D., Jr., and Bookhout, C. G. (1959). The larval development of *Callinectes sapidus* Rathbun reared in the laboratory. *Biol. Bull. (Woods Hole, Mass.)* **116,** 373–396.

Costlow, J. D., Jr., and Bookhout, C. G. (1960). The complete larval development of *Sesarma cinereum* (Bosc) reared in the laboratory. *Biol. Bull. (Woods Hole, Mass.)* **118,** 203–214.

Costlow, J. D., Jr., and Bookhout, C. G. (1962). The larval development of *Sesarma reticulatum* Say reared in the laboratory. *Crustaceana (Leiden)* **4,** 281–294.

Costlow, J. D., Jr., and Bookhout, C. G. (in press). Second generation pesticides and crab development. *Environ. Prot. Agency, Proc. Symp. Environ. Res.*

Costlow, J. D., Jr., Rees, G. H., and Bookhout, C. G. (1959). Preliminary note on the complete larval development of *Callinectes sapidus* Rathbun under laboratory conditions. *Limnol. Oceanogr.* **4,** 222–223.

Costlow, J. D., Jr., Bookhout, C. G., and Monroe, R. (1960). The effect of salinity and temperature on larval development of *Sesarma cinereum* (Bosc) reared in the laboratory. *Biol. Bull. (Woods Hole, Mass.)* **118,** 183–202.

Costlow, J. D., Jr., Bookhout, C. G., and Monroe, R. (1962). Salinity–temperature effects on the larval development of the crab *Panopeus herbstii* Milne-Edwards, reared in the laboratory. *Physiol. Zool.* **35,** 79–93.

Costlow, J. D., Jr., Bookhout, C. G., and Monroe, R. J. (1966). Studies on the larval development of the crab, *Rhithropanopeus harrisii* (Gould). 1. The effect of salinity and temperature on larval development. *Physiol. Zool.* **39,** 81–100.

Crane, J. (1975). "Fiddler Crabs of the World. Ocypodidae: Genus *Uca.*" Princeton Univ. Press, Princeton, New Jersey.

Crichton, O. W. (1960). Marsh crab, intertidal tunnel-maker and grass-eater. *Estuarine Bull.* **5,** 3–10.

Crichton, O. (1974). Caloric studies of *Spartina* and the marsh crab *Sesarma reticulatum* (Say). *In* "Coastal Ecological Systems of the United States" (H. T. Odum, B. J. Copeland, and E. A. McMahan, eds.), Vol. II, pp. 99–149. Coastal Conserv. Found., Washington, D. C.

Cripe, C. R., and Livingston, R. J. (1977). Dynamics of mirex and its principal photoproducts in a simulated marsh system. *Arch. Environ. Contam. Toxicol.* **5,** 295–303.

Crothers, J. H. (1967). The biology of the shore crab *Carcinus maenas* (L.). 1. The background-anatomy, growth and life history. *Field Stud.* **2,** 407–434.

Crothers, J. H. (1968). The biology of the shore crab *Carcinus maenas* (L.). 2. The life of the adult crab. *Field Stud.* **2,** 579–614.

Crothers, J. H. (1969). The distribution of crabs in Dale Roads (Milford Haven, Pembrokeshire) during summer. *Field Stud.* **3,** 109–124.

Crothers, J. H. (1970). The distribution of crabs on rocky shores around the Dale Peninsula. *Field Stud.* **3,** 263–274.

Darnell, R. M. (1959). Studies of the life history of the blue crab (*Callinectes sapidus* Rathbun) in Louisiana waters. *Trans. Am. Fish. Soc.* **88,** 294–304.

Darnell, R. M. (1961). Trophic spectrum of an estuarine community, based on studies of Lake Pontchartrain, Louisiana. *Ecology* **42,** 553–568.

Day, J. W., Jr., Smith, W. G., Wagner, P. R., and Stowe, W. C. (1973). Community structure and carbon budget of a salt marsh and shallow bay estuarine system in Louisiana. *La. State Univ., Cent. Wetland Resour., Publ.* **LSU-SG-72-04,** 1–80.

Dean, J. M., and Vernberg, F. J. (1965). Variations in the blood glucose level of Crustacea. *Comp. Biochem. Physiol.* **14,** 29–34.

Dean, J. M., and Vernberg, F. J. (1966). Hypothermia and blood of crabs. *Comp. Biochem. Physiol.* **17,** 19–22.

DeCoursey, P. J., and Vernberg, W. B. (1972). Effect of mercury on survival, metabolism, and behavior of larval *Uca pugilator*. *Oikos* **23,** 241–247.

Deevey, G. B. (1960). The zooplankton of the surface waters of the Delaware Bay region. *Bull. Bingham Oceanogr. Collect.* **17,** 5–53.

Dehnel, P. A. (1960). Effect of temperature and salinity on the oxygen consumption of two intertidal crabs. *Biol. Bull. (Woods Hole, Mass.)* **118,** 215–249.

Dehnel, P. A. (1962). Aspects of osmoregulation in two species of intertidal crabs. *Biol. Bull. (Woods Hole, Mass.)* **122,** 208–227.

Dehnel, P. A. (1966). Chloride regulation in the crab *Hemigrapsus nudus*. *Physiol. Zool.* **39,** 259–265.

Dehnel, P. A., and Stone, D. (1964). Osmoregulatory role of the antennary gland in two species of estuarine crabs. *Biol. Bull. (Woods Hole, Mass.)* **126,** 354–372.

Démeusy, N. (1957). Respiratory metabolism of the fiddler crab *Uca pugilator* from two different latitudinal populations. *Biol. Bull. (Woods Hole, Mass.)* **113,** 245–253.

Dolan, C. W., Savage, I. F., and Clark, R. C., Jr. (1970). "Environmental Statement on the Proposed Leasing of Puget Sound Shorelands and Beds of Navigable Waters for Oil and Gas Exploration." Submitted by the Joint Committee to the State of Washington Board of Natural Resources, October, 1970.

Dries, M., and Adelung, D. (1976). Neue Ergebnisse über die Afzucht von *Carcinus maenas* im Laboratorium. *Mar. Biol.* **38,** 17–24.

Dudley, D. L., and Judy, M. H. (1971). Occurrence of larval, juvenile, and mature crabs in the vicinity of Beaufort Inlet, North Carolina. *NOAA Tech. Rep., NMFS SSRF* **637,** 1–10.

Duke, T., Willis, J., Price, T., and Fischler, K. (1967). "Influence of Environmental Factors on the Concentration of ^{65}Zn by an Experimental Community," pp. 355–362. Bur. Commer. Fish., Radiobiol. Lab., Beaufort, North Carolina.

Dunnington, E. A. (1956). Blue crabs observed to dig soft shell clams for food. *Md. Tidewater News* **12,** 1, 4.

Edmondson, C. H. (1962). Xanthidae of Hawaii. *Occas. Pap. Bishop Mus.* **22,** 215–309.

Edwards, G. A. (1950). The influence of eyestalk removal on the metabolism of the fiddler crab. *Physiol. Comp. Oecol.* **2,** 34–50.

Eisler, R. (1971). Cadmium poisoning in *Fundulus heteroclitus* (Pisces: Cyprinodontidae) and other marine organisms. *J. Fish. Res. Board Can.* **28,** 1225–1234.

Engel, D. W. (1967). Effect of single and continuous exposures of gamma radiation on the survival and growth of the blue crab, *Callinectes sapidus*. *Radiat. Res.* **32,** 685–691.

Engel, D. W. (1973). The radiation sensitivities of three species of fiddler crabs, *Uca pugilator, U. pugnax* and *U. minax*. *Chesapeake Sci.* **14,** 289–291.

Engel, D. W. (1977). Comparison of the osmoregulatory capabilities of two portunid crabs, *Callinectes sapidus* and *C. similis*. *Mar. Biol.* **41,** 275–279.

Engel, D. W. (1979). "Methodology of Radiation Effects Experimentation Aquatic Organisms and Ecosystems. Experimental Approaches to Demonstrate the Interactions of Radiation with Other Environmental Stresses." International Atomic Energy Agency, Vienna (in press).

Engel, D. W., Davis, E. M., Angelovic, J. W., and Smith, D. E. (1973). Effect of radiation, salinity, and temperature on the ionic regulation of the blue crab *Callinectes sapidus*. *In* "Proceedings of the Third National Symposium on Radiology," Conf-710510-P2, pp. 113–117. U. S. At. Energy Comm. Oak Ridge, Tennessee.

Epifanio, C. E. (1971). Effects of dieldrin in seawater on the development of two species of crab larvae, *Leptodius floridanus* and *Panopeus herbstii*. *Mar. Biol.* **11,** 356–362.

Epifanio, C. E. (1973). Dieldrin uptake by larvae of the crab *Leptodius floridanus*. *Mar. Biol.* **19,** 320–322.

Evans, P. D., and Mann, K. H. (1977). Selection of prey by American lobsters (*Homarus americanus*) when offered a choice between sea urchins and crabs. *J. Fish. Res. Board Can.* **34,** 2203–2207.

Fischler, K. J., and Walburg, C. H. (1962). Blue crab movement in coastal South Carolina, 1958–59. *Trans. Am. Fish. Soc.* **91,** 275–278.

Forward, R. B., Jr., and Costlow, J. D., Jr. (1976). Crustacean larval behavior as an indicator of sublethal effects of an insect juvenile hormone mimic. *In* "Estuarine Processes" (M. Wiley, ed.), Vol. 1, pp. 279–289. Academic Press, New York.

Foskett, J. K. (1977). Osmoregulation in the larvae and adults of the grapsid crab *Sesarma reticulatum* Say. *Biol. Bull. (Woods Hole, Mass.)* **153,** 505–526.

Fowler, B. A., Fay, R. C., Walter, R. L., Willis, R. D., and Gutknecht, W. F. (1975). Levels of toxic metals in marine organisms collected from southern California coastal waters. *Environ. Health Perspect.* **12,** 71–76.

Gadzhiev, D. V. (1963). Dutch crab in the Caspian Sea. (Gollandskii krab v Kaspiiskom more.) *Priroda (Moscow)* **10,** 126.

Gallaway, B. J., and Strawn, K. (1975). Seasonal abundance and distribution of the blue crab, *Callinectes sapidus* Rathbun, in the discharge area of the P. H. Robinson Generating Station, Galveston Bay, Texas. *Tex. J. Sci.* **26,** 185–202.

Glude, J. B. (1975). The effects of temperature and predators on the abundance of the soft-shell clam, *Mya arenaria* in New England. *Trans. Am. Fish. Soc.* **84,** 13–26.

Gray, I. E. (1957). A comparative study of the gill area of crabs. *Biol. Bull. (Woods Hole, Mass.)* **112,** 34–42.

Guinot, D. (1968). Recherches préliminaires sur les groupements naturels chez les Crustacés Décapodes Brachyoures. IV. Observations sur quelques genres de Xanthidae. *Bull. Mus. Hist. Nat., Paris* [2] **39,** 695–727.

Haefner, P. A., Jr. (1976). Distribution, reproduction and moulting of the rock crab, *Cancer irroratus* Say, 1817, in the mid-Atlantic Bight. *J. Nat. Hist.* **10,** 377–397.

Haefner, P. A., Jr., and Shuster, C. N., Jr. (1964). Length increments during terminal molt of the female blue crab, *Callinectes sapidus*, in different salinity environments. *Chesapeake Sci.* **5,** 114–118.

Haefner, P. A., Jr., and Van Engel, W. A. (1975). Aspects of molting, growth and survival of male rock crabs, *Cancer irroratus*, in Chesapeake Bay. *Chesapeake Sci.* **16,** 253–265.

Hamilton, P. V. (1976). Predation on *Littorina irrorata* (Mollusca: Gastropoda) by *Callinectes sapidus* (Crustacea: Portunidae). *Bull. Mar. Sci.* **26,** 403–409.

Hart, J. F. L. (1935). The larval development of British Columbia Brachyura. I. Xanthidae, Pinnotheridae (in part), and Grapsidae. *Can. J. Res.* **12,** 411–432.

Hart, J. F. L. (1968). Crab-like Anomura and Brachyura (Crustacea: Decapoda) from southeastern Alaska and Prince William Sound. *Nat. Mus. Can. Nat. Hist. Pap.* No. 38, pp. 1–6.

Hartnoll, R. G. (1969). Mating in the Brachyura. *Crustaceana (Leiden)* **16,** 161–181.

Hazlett, B., Bach, C., and Mitchell, C. (1977). Distributional patterns of the xanthid crab *Catalepstodius floridanus* (Gibbes, 1850) (Decapoda, Brachyura, Xanthidae). *Crustaceana (Leiden)* **33,** 316–319.

Heard, R. W. (1975). Feeding habits of white catfish from a Georgia estuary. *Fla. Sci.* **38,** 20–28.

Hedgpeth, J. W. (1950). Notes on the marine invertebrate fauna of salt flat areas in Aransas National Wildlife Refuge, Texas. *Publ. Inst. Mar. Sci.* **1,** 103–119.

Herman, S. S., Mihursky, J. A., and McErlean, A. J. (1968). Zooplankton and environmental characteristics of the Patuxent River estuary 1963–1965. *Chesapeake Sci.* **9,** 67–82.

Herrnkind, W. F. (1968a). The breeding of *Uca pugilator* (Bosc) and mass rearing of the larvae with comments on the behavior of the larval and early crab stages (Brachyura, Ocypodidae). *Crustaceana (Leiden), Suppl.* **2,** 214–224.

Herrnkind, W. F. (1968b). Adaptive visually-directed orientation in *Uca pugilator*. *Am. Zool.* **8,** 585–598.

Herrnkind, W. F. (1972). Orientation in shore living arthropods, especially the sand fiddler crab. *In* "Behavior of Marine Animals, Current Perspectives in Research" (H. E. Winn and B. L. Olla, eds.), Vol. I, pp. 1–59. Plenum, New York.

Hillman, N. S. (1964). Studies on the distribution and abundance of decapod larvae in Narragansett Bay, Rhode Island, with consideration of morphology and mortality. M.S. Thesis, University of Rhode Island, Kingston.

Hoopes, D. T. (1973). Alaska's Fishery Resources—The Dungeness Crab. *Fish. Facts-* **6,** 1–14. Natl. Oceanic Atmo. Adm. Natl. Mar. Fish. Serv., Washington, D.C.

Hutcheson, M. S. (1974). The effect of temperature and salinity on cadmium uptake by the blue crab, *Callinectes sapidus*. *Chesapeake Sci.* **15,** 237–241.

Hyman, O. W. (1920). The development of *Gelasimus* after hatching. *J. Morphol.* **33,** 485–501.

Jeffries, H. P. (1966). Partitioning of the estuarine environment by two species of *Cancer*. *Ecology* **47,** 477–481.

Johansen, K., Lenfant, C., and Mecklenburg, T. A. (1970). Respiration in the crab, *Cancer magister*. *Z. Vergl. Physiol.* **70,** 1–19.

Jones, L. L. (1941). Osmotic regulation in several crabs of the Pacific coast of North America. *J. Cell. Comp. Physiol.* **18,** 179–192.

Kalber, F. A. (1970). Osmoregulation in decapod larvae as a consideration in culture techniques. *Helgol. Wiss. Meeresunters.* **20,** 697–706.

Kalber, F. A., Jr., and Costlow, J. D., Jr. (1966). The ontogeny of osmoregulation and its neurosecretory control in the decapod crustacean, *Rhithropanopeus harrisii* (Gould). *Am. Zool.* **6,** 221–229.

Kalber, F. A., Jr., and Costlow, J. D., Jr. (1968). Osmoregulation in larvae of the land-crab, *Cardisoma guanhumi* Latreille. *Am. Zool.* **8,** 411–416.

King, B. D., III (1971). Study of migratory patterns of fish and shellfish through a natural pass. *Tex. Parks Wildl. Dep., Tech. Ser.* No. 9, pp. 1–54.

Kinne, O. (1964). The effects of temperature and salinity on marine and brackish water animals. *Oceanogr. Mar. Biol.* **2,** 281–339.

Knieper, L. H., and Culley, D. D., Jr. (1975). The effects of crude oil on the palatability of marine crustaceans. *Prog. Fish Cult.* **37,** 9–14.

Knudsen, J. W. (1964). Observations of the reproductive cycles and ecology of the common Brachyura and crablike Anomura of Puget Sound, Washington. *Pac. Sci.* **18,** 3–33.

Koenig, C. C., Livingston, R. J., and Cripe, C. R. (1976). Blue crab mortality: Interaction of temperature and DDT residues. *Arch. Environ. Contam. Toxicol.* **4,** 119–128.

Kraeuter, J. N., and Wolf, P. L. (1974). The relationship of marine macroinvertebrates to salt marsh plants. *In* "Ecology of Halophytes" (R. J. Reimold and W. H. Queen, eds.), pp. 449–462. Academic Press, New York.

Krebs, C. T., Valiela, I., Harvey, G. R., and Teal, J. M. (1974). Reduction of field populations of fiddler crabs by uptake of chlorinated hydrocarbons. *Mar. Pollut. Bull.* **5,** 140–142.

Kurian, C. B. (1956). Larvae of decapod Crustacea from the Adriatic Sea. *Acta Adriat.* **6,** 1–108.

Lance, J. (1964). The salinity tolerances of some estuarine planktonic crustaceans. *Biol. Bull. (Woods Hole, Mass.)* **127,** 108–118.

Landers, W. S. (1954). Notes on the predation of the hard clam *Venus mercenaria* by the mud crab, *Neopanope texana*. *Ecology* **35,** 422.

Leahy, T. M. (1975). How big is a crab's world? *Sea Grant 70's, NOAA* **5,** 1–2.

Lee, R. F., Ryan, C., and Neuhauser, M. L. (1976). Fate of petroleum hydrocarbons taken up from food and water by blue crab *Callinectes sapidus*. *Mar. Biol.* **37,** 363–370.

Leffler, C. W. (1972). Some effects of temperature on the growth and metabolic rate of juvenile blue crabs, *Callinectes sapidus*, in the laboratory. *Mar. Biol.* **14,** 104–110.

Leffler, C. W. (1975). Effects of ingested mirex and DDT on juvenile *Callinectes sapidus* Rathbun. *Environ. Pollut.* **8,** 238–300.

Lowe, J. I. (1965). Chronic exposure of blue crabs, *Callinectes sapidus*, to sublethal concentrations of DDT. *Ecology* **46,** 899–900.

Lowe, J. I., Parrish, P. R., Wilson, A. J., Jr., Wilson, P. D., and Duke, T. W. (1971). Effects of mirex on selected estuarine organisms. *Trans. North Am. Wildl. Nat. Resour. Conf.* **36,** 171–186.

Lunz, G. R. (1937). Xanthidae (mud crabs) of the Carolinas. *Charleston Mus. Leafl.* No. 9, pp. 1–27.

Lynch, M. P. (1974). The use of physiological indicators of stress in marine invertebrates as a tool for marine pollution monitoring. *Mar. Technol. Soc. J.* **10,** 881–890.

McDermott, J. J. (1960). The predation of oysters and barnacles by crabs of the family Xanthidae. *Proc. Pa. Acad. Sci.* **34,** 199–211.

McDermott, J. J., and Flower, F. B. (1952). Preliminary studies of the common mud crabs on oyster beds of Delaware Bay. *Natl. Shellfish Assoc. Conv. Addresses, 1952* pp. 47–50.

McKenzie, M. D. (1970). "Fluctuations in Abundance of the Blue Crab and Factors Affecting Mortalities," Tech. Rep. No. 1, Mar. Resour. Div. PL88-309, Proj. No. 2-79-R-1. South Carolina Wildl. Resour. Dep., Charleston.

McWhinnie, M. A., and Scheer, B. T. (1958). Blood glucose of the crab *Hermigrapsus nudus*. *Science* **128,** 90.

Mahood, R. K., McKenzie, M. D., Middaigh, D. P., Bollar, S. J., and Davis, J. R. (1970). "A Report on the Cooperative Blue Crab Study—South Atlantic States." Coastal Fish. Div. Contrib. Ser. No. 1. Georgia Game Fish Comm., Brunswick.

Makarov, Yu. N. (1977). Some aspects of the ecology of decapod larvae of the Black Sea and Sea of Azov. *Oceanology (Engl. Transl.)* **16,** 611–613.

Mann, K. H. (1973). Seaweeds: Their productivity and strategy for growth. *Science* **182,** 975–981.

Marganian, V. M., and Wall, W. J., Jr. (1972). Dursban and diazinon residues in biota following treatment of intertidal plots on Cape Cod 1967–69. *Pestic. Monit. J.* **6,** 160–165.

Marsh, G. A. (1973). The *Zostera* epifaunal community in the York River, Virginia. *Chesapeake Sci.* **14,** 87–97.

Maugh, T. H. (1978). Chemicals: How many are there? *Science* **199,** 162.

Meenahshi, V. R., and Scheer, B. T. (1960). Metabolism of glucose in the crabs *Cancer magister* and *Hemigrapsus nudus*. *Anat. Rec.* **137,** 381.

Melzian, B. D. (1977). "The Exposure of Blue Crabs, *Callinectes sapidus*, to Water Soluble Hydrocarbons Derived from #2 Fuel Oil," Annu. Rep., U.S. Environ. Prot. Agency, Environ. Res. Lab., Narragansett, Rhode Island.

Menzel, R. W., and Hopkins, S. H. (1956). Crabs as predators of oysters in Louisiana. *Proc. Natl. Shellfish. Assoc.* **46,** 177–184.

Menzel, R. W., and Nichy, F. W. (1958). Studies of the distribution and feeding habits of some oyster predators in Alligator Harbor, Florida. *Bull. Mar. Sci. Gulf Caribb.* **8,** 125–145.

Mihursky, J. A., Kennedy, V. S., McErlean, A. J., Roosenburg, W. H., and Gatz, A. J. (1974). The thermal requirements and tolerances of key estuarine organisms. *Tech. Rep. Water Resour. Res. Cent., Univ. Md.*, **26,** 1–153.

Miller, D. C. (1961). The feeding mechanism of fiddler crabs, with ecological considerations of feeding adaptations. *Zoologica (N.Y.)* **46,** 89–100.

Miller, K. G., and Maurer, D. (1973). Distribution of the fiddler crabs, *Uca pugnax* and *Uca minax*, in relation to salinity in Delaware rivers. *Chesapeake Sci.* **14,** 219–221.

Modin, J. C. (1969). Residues in fish, wildlife and estuaries. *Pestic. Monit. J.* **3,** 1–7.

Mootz, C. A., and Epifanio, C. E. (1974). An energy budget for *Menippe mercenaria* larvae fed *Artemia* nauplii. *Biol. Bull. (Woods Hole, Mass.)* **146,** 44–55.

More, W. R. (1969). A contribution to the biology of the blue crab (*Callinectes sapidus* Rathbun) in Texas, with a description of the fishery. *Tex. Parks Wildl. Dep., Tech. Ser.* No. 1, pp. 1–31.

Musick, J. A., and McEachran, J. D. (1972). Autumn and winter occurrence of decapod crustaceans in Chesapeake Bight, U.S.A. *Crustaceana (Leiden)* **22,** 190–200.

Nations, J. D. (1975). The genus *Cancer* (Crustacea: Brachyura): Systematics, biogeography and fossil record. *Nat. Hist. Mus., Los Angeles City Sci. Bull.* No. 23, 1–104.

Naylor, E. (1960). A North American xanthid crab new to Britain. *Nature (London)* **187,** 256–257.

Naylor, E., and Isaac, M. J. (1973). Behavioural significance of pressure responses in megalopa larvae of *Callinectes sapidus* and *Macropipus* sp. *Mar. Behav. Physiol.* **1,** 341–350.

Nichols, P. R., and Keney, P. M. (1963). Crab larvae (*Callinectes*), in plankton collections from cruises of M/V *Theodore N. Gill*, South Atlantic coast of the United States, 1953–54. *U. S., Fish Wildl. Serv., Spec. Sci. Rep.—Fish.* No. 448, pp. 1–14.

Odum, H. T. (1953). Factors controlling marine invasion into Florida fresh waters. *Bull. Mar. Sci. Gulf Caribb.* **3,** 134–156.

Odum, W. E., and Heald, E. J. (1972). Trophic analyses of an estuarine mangrove community. *Bull. Mar. Sci.* **22,** 671–738.

O'Hara, J. (1973). Cadmium uptake by fiddler crabs exposed to temperature and salinity stress. *J. Fish. Res. Board Can.* **30,** 846–848.

Ong, Kah-sin, and Costlow, J. D., Jr. (1970). The effect of salinity and temperature on the larval development of the stone crab, *Menippe mercenaria* (Say) reared in the laboratory. *Chesapeake Sci.* **11,** 16–29.

Parchevskii, V. P., and Sokolova, I. A. (1971). Strontium-90 content of some Black Sea organisms in 1965–1968. *Dokl. Akad. Nauk SSSR* **199,** 69–71.

Parsons, T. R., Bawden, C. A., and Heath, W. A. (1973). Preliminary survey of mercury and other metals contained in animals from the Fraser River mudflats. *J. Fish. Res. Board Can.* **30,** 1014–1016.

Pearse, A. S. (1914). On the habits of the *Uca pugnax* (Smith) and *U. pugilator* (Bosc). *Trans. Wis. Acad. Sci., Arts Lett.* **17,** 791–802.

60

Pearson, J. C. (1948). Fluctuations in the abundance of the blue crab in Chesapeake Bay. *Fish Wildl. Serv. (U.S.), Res. Rep.* No. 14, 1–26.

Pearson, W. H., and Olla, B. L. (1977). Chemoreception in the blue crab, *Callinectes sapidus*. *Biol. Bull. (Woods Hole, Mass.)* **153,** 346–354.

Petrocelli, S. R., Anderson, J. W., and Hanks, A. R. (1974). DDT and dieldrin residues in selected biota from San Antonio Bay, Texas, 1972. *Pestic. Monit. J.* **8,** 167–172.

Petrocelli, S. R., Anderson, J. W., and Hanks, A. R. (1975). Biomagnification of dieldrin residues by food-chain transfer from clams to blue crabs under controlled conditions. *Bull. Environ. Contam. Toxicol.* **13,** 108–116.

Pinschmidt, W. C. (1964). Distribution of crab larvae in relation to some environmental conditions in the Newport River estuary, North Carolina. *Diss. Abstr.* **24,** 4883.

Poole, R. L. (1966). A description of laboratory-reared zoeae of *Cancer magister* Dana, and megalopae taken under natural conditions (Decapoda, Brachyura). *Crustaceana (Leiden)* **11,** 83–97.

Poole, R. L. (1967). Preliminary results of the age and growth study of the market crab (*Cancer magister*) in California: The age and growth of *Cancer magister* in Bodega Bay. *In* "Proceedings of the Symposium on Crustacea held at Ernakulam, Jan. 12–15, 1965," Part II, pp. 553–567. Mar. Biol. Assoc. India, Mar. Fish. P. O., Mandapam Camp.

Porter, H. J. (1960). Zoeal stages of the stone crab, *Menippe mercenaria* Say. *Chesapeake Sci.* **1,** 168–177.

Powell, E. H., Jr., and Gunter, G. (1968). Observations on the stone crab *Menippe mercenaria* Say, in the vicinity of Port Aransas, Texas. *Gulf Res. Rep.* **2,** 285–299.

Rasmussen, E. (1959). Behaviour of sacculinized shore crabs (*Carcinus maenas* Pennant). *Nature (London)* **183,** 479–480.

Rasmussen, E. (1973). Systematics and ecology of the Isefjord marine fauna (Denmark). *Ophelia* **11,** 1–495.

Rathbun, M. J. (1918). The grapsoid crabs of America. *U.S. Natl. Mus., Bull.* **97,** 1–461.

Rathbun, M. J. (1930). The cancroid crabs of America of the families Euryalidae, Portunidae, Atelecyclidae, Cancridae and Xanthidae. *U.S. Natl. Mus., Bull.* **152,** 1–609.

Reed, P. H. (1969). Culture methods and effects of temperature and salinity on survival and growth of Dungeness crab (*Cancer magister*) larvae in the laboratory. *J. Fish. Res. Board Can.* **26,** 389–397.

Rees, G. H. (1962). Effects of gamma radiation on two decapod crustaceans, *Palaemonetes pugio* and *Uca pugnax*. *Chesapeake Sci.* **3,** 29–34.

Rice, A. L., and Ingle, R. W. (1975). The larval development of *Carcinus maenas* (L.) and *C. mediterraneus* Czerniavsky (Crustacea, Brachyura, Portunidae) reared in the laboratory. *Bull. Br. Mus. (Nat. Hist.), Zool.* **28,** 103–119.

Robinson, L. A., ed. (1977). "Fisheries Statistics of the United States, 1976," Curr. Fish. Statist. No. 7200. Natl. Oceanic Atmo. Adm., Natl. Mar. Fish. Serv., U.S. Dept. of Commerce, Washington, D.C. 96 pp.

Ropes, J. W. (1968). The feeding habits of the green crab, *Carcinus maenas* (L.). *Fish. Bull.* **67,** 183–203.

Ryan, E. P. (1956). Observations on the life histories and the distribution of the Xanthidae (mud crabs) of Chesapeake Bay. *Am. Midl. Nat.* **56,** 138–162.

Salmon, M., and Atsaides, S. P. (1968). Behavioral, morphological and ecological evidence for two new species of fiddler crabs (genus *Uca*) from the Gulf coast of the United States. *Proc. Biol. Soc. Wash.* **81,** 275–290.

Salmon, M., and Horch, K. W. (1972). Acoustic signalling and detection by semiterrestrial crabs of the family Ocypodidae. *In* "Behavior of Marine Animals, Current Perspectives in Research" (H. E. Winn and B. L. Olla, eds.), Vol. 1, pp. 60–96. Plenum, New York.

Sandifer, P. A. (1973). Distribution and abundance of decapod crustacean larvae in the York River estuary and adjacent lower Chesapeake Bay, Virginia, 1968–1969. *Chesapeake Sci.* **14,** 235–257.

Sandifer, P. A. (1975). The role of pelagic larvae in recruitment to populations of adult decapod crustaceans in the York River estuary and adjacent lower Chesapeake Bay, Virginia. *Estuarine Coastal Mar. Sci.* **3,** 269–279.

Sastry, A. N. (1977). The larval development of the rock crab, *Cancer irroratus* Say, 1817, under laboratory conditions (Decapoda Brachyura). *Crustaceana (Leiden)* **32,** 155–168.

Savage, T. (1971). Mating of the stone crab, *Menippe mercenaria* (Say) (Decapoda, Brachyura). *Crustaceana (Leiden)* **20,** 315–316.

Scarratt, D. J., and Lowe, R. (1972). Biology of rock crab (*Cancer irroratus*) in Northumberland Strait. *J. Fish. Res. Board Can.* **29,** 161–166.

Schimmel, S. C., Patrick, J. M., Faas, L. F., Oglesby, J. L., and Wilson, A. J., Jr. (1979). Kepone®: Toxicity to and bioaccumulation by blue crabs. *Estuaries* **2,** 9–15.

Schoor, W. P. (1974). Accumulation of mirex-14C in the adult blue crab (*Callinectes sapidus*). *Bull. Environ. Contam. Toxicol.* **12,** 136–137.

Schwartz, B., and Safir, S. R. (1915). The natural history and behavior of the fiddler crab. *Cold Spring Harbor Monogr.* **8,** 1–24.

Seiple, W. (1979). Distribution, habitat preferences and breeding periods in the crustaceans *Sesarma cinereum* and *S. reticulatum* (Brachyura: Decapoda Grapsidae). *Mar. Biol.* **52,** 77–86.

Sheridan, P. F. (1975). Uptake, metabolism, and distribution of DDT in organs of the blue crab, *Callinectes sapidus*. *Chesapeake Sci.* **16,** 20–26.

Sikora, W. B., Heard, R. W., and Dahlberg, M. D. (1972). The occurrence and food habits of two species of hake, *Urophycis regius* and *U. floridanus* in Georgia estuaries. *Trans. Am. Fish. Soc.* **101,** 513–525.

Sloan, J. P., Thompson, J. A. J., and Larkin, P. A. (1974). Biological half-life of inorganic mercury in the Dungeness crab (*Cancer magister*). *J. Fish. Res. Board Can.* **31,** 1571–1576.

Smith, R. I. (1967). Osmotic regulation and adaptive reduction of water-permeability in brackish-water crab, *Rhithropanopeus harrisi* (Brachyura, Xanthidae). *Biol. Bull. (Woods Hole, Mass.)* **133,** 643–658.

Snow, C. D., and Nielsen, J. R. (1966). Premating and mating behavior of the Dungeness crab (*Cancer magister* Dana). *J. Fish. Res. Board Can.* **23,** 1319–1323.

Squires, H. J. (1965). Decapod crustaceans of Newfoundland, Labrador and the Canadian eastern Arctic. *Fish. Res. Board Can., Rep. Ser. (Biol.)* No. 810, pp. 1–212.

Subrahmanyam, C. B., Kruczynski, W. L., and Drake, S. H. (1976). Studies on the animal communities in two north Florida salt marshes. Part II. Macroinvertebrate communities. *Bull. Mar. Sci.* **26,** 172–195.

Sulkin, S. D., and Epifanio, C. E. (1975). Comparison of rotifers and other diets for rearing early larvae of the blue crab, *Callinectes sapidus* Rathbun. *Estuarine Coastal Mar. Sci.* **3,** 109–113.

Sulkin, S. D., and Norman, K. (1976). A comparison of two diets in the laboratory culture of the zoeal stages of the brachyuran crabs *Rhithropanopeus harrisii* and *Neopanope* sp. *Helgol. Wiss. Meeresunters.* **28,** 183–190.

Swartz, R. C. (1972). Postlarval growth and reproductive biology of the xanthid crab, *Neopanope texana sayi*. *Diss. Abstr.* **33,** 7150–7151B.

Tagatz, M. E. (1968). Biology of the blue crab, *Callinectes sapidus* Rathbun, in the St. Johns River, Florida. *Fish. Bull.* **67,** 17–33.

Tagatz, M. E. (1969). Some relations of temperature acclimation and salinity to thermal tolerance of the blue crab, *Callinectes sapidus*. *Trans. Am. Fish. Soc.* **98,** 713–716.

Tagatz, M. E., and Hall, A. B. (1971). Annotated bibliography on the fishing industry and biology of the blue crab, *Callinectes sapidus*, *NOAA Tech. Rep., NMFS SSRF* No. 640, 1–94.

Tagatz, M. E., Borthwick, P. W., Cook, G. H., and Coppage, D. L. (1974). Effects of ground applications of malathion on salt-marsh environments in northwestern Florida. *Mosq. News* **34,** 309–315.

Tagatz, M. E., Borthwick, P. W., and Forester, J. (1975). Seasonal effects of leached mirex on selected estuarine animals. *Arch. Environ. Contam. Toxicol.* **3,** 371–383.

Takahashi, F. T., and Kittredge, J. S. (1973). Sublethal effects of the water soluble component of oil: Chemical communication in the marine environment. *La. State Univ., Cent. Wetland Resour., Publ.* **LSU-SG-73-01,** 259–264.

Teal, J. M. (1958). Distribution of fiddler crabs in Georgia salt marshes. *Ecology* **39,** 185–193.

Teal, J. M. (1959). Respiration of crabs in Georgia salt marshes and its relation to their ecology. *Physiol. Zool.* **32,** 1–14.

Teal, J. M., and Carey, F. G. (1967). The metabolism of marsh crabs under conditions of reduced oxygen pressure. *Physiol. Zool.* **40,** 83–91.

Tennant, D. A., and Forster, W. O. (1969). Seasonal variation and distribution of ^{65}Zn, ^{54}Mn and ^{51}Cr in tissues of the crab *Cancer magister* Dana. *Health Phys.* **18,** 649–657.

Thurberg, F. P., Dawson, M. A., and Collier, R. S. (1973). Effects of copper and cadmium on osmoregulation and oxygen consumption in two species of estuarine crabs. *Mar. Biol.* **23,** 171–175.

Todd, M.-E., and Dehnel, P. A. (1960). Effect of temperature and salinity on heat tolerance in two grapsoid crabs, *Hemigrapsus nudus* and *Hemigrapsus oregonensis*. *Biol. Bull. (Woods Hole, Mass.)* **118,** 150–172.

Toombs, G. L. (1965). Radiological survey of the lower Columbia River in Oregon, August 1963–July 1964. *Radiol. Health Data* **6,** 563–568.

Turner, H. J., Jr. (1953). The edible crab fishery of Massachusetts. *In* "Sixth Report on Investigations of the Shellfisheries of Massachusetts," pp. 25–28. Dept. Nat. Resour., Div. Mar. Fish., Woods Hole Oceanogr. Inst., Woods Hole, Massachusetts.

Turner, H. J., Jr. (1954). The edible crab fishery of Boston Harbor. *In* "Seventh Report on Investigations of the Shellfisheries of Massachusetts," pp. 7–16. Dept. Nat. Resour., Div. Mar. Fish., Woods Hole Oceanogr. Inst., Woods Hole, Massachusetts.

Valiela, I., Babiec, D. F., Atherton, W., Seitzinger, S., and Krebs, C. (1974). Some consequences of sexual dimorphism: Feeding in male and female fiddler crabs, *Uca pugnax* (Smith). *Biol. Bull. (Woods Hole, Mass.)* **147,** 652–660.

Van Engel, W. A. (1958). The blue crab and its fishery in Chesapeake Bay. *Commer. Fish. Rev.* **20,** 6–17.

Vernberg, F. J. (1959). Studies on the physiological variation between tropical and temperate zone fiddler crabs of the genus *Uca*. II. Oxygen consumption of whole organisms. *Biol. Bull. (Woods Hole, Mass.)* **117,** 163–184.

Vernberg, F. J., and Costlow, J. D., Jr. (1966). Studies on the physiological variation between tropical and temperate-zone fiddler crabs of the genus *Uca*. IV. Oxygen consumption of larvae and young crabs reared in the laboratory. *Physiol. Zool.* **39,** 36–52.

Vernberg, F. J., and Tashian, R. E. (1959). Studies on the physiological variation between tropical and temperate zone fiddler crabs of the genus *Uca*. I. Thermal death limits. *Ecology* **40,** 589–593.

Vernberg, F. J., and Vernberg, W. B. (1970). Lethal limits and the zoogeography of the faunal assemblages of coastal Carolina waters. *Mar. Biol.* **6,** 26–32.

Vernberg, W. B., and DeCoursey, P. J. (1977). Effects of sublethal metal pollutants on the fiddler crab, *Uca pugilator*. *U.S. Environ. Prot. Agency, Off. Res. Dev. [Rep.] EPA* **EPA-600/3-77-024,** 215–220.

Vernberg, W. B., and O'Hara, J. (1972). Temperature-salinity stress and mercury uptake in the fiddler crab, *Uca pugilator*. *J. Fish. Res. Board Can.* **29,** 1491–1494.

61

Vernberg, W. B., and Vernberg, F. J. (1972). Synergistic effects of temperature, salinity, and mercury on survival and metabolism of the adult fiddler crab, *Uca pugilator*. *Fish. Bull.* **70,** 415–420.

von Hagen, H. O. (1976). Review. Jocelyn Crane, "Fiddler Crabs of the World. Ocypodidae: Genus *Uca*," ISBN 08102-6. Princeton University Press, Princeton, New Jersey, 1975. *Crustaceana (Leiden)* **31,** 221–224.

Waldron, K. D. (1958). The fishery and biology of the Dungeness crab (*Cancer magister* Dana) in Oregon waters. *Contrib., Fish Comm. Ore.* No. **24,** 1–43.

Walton, E., and Williams, A. B. (1971). Reef populations of mud crabs and snapping shrimp. *In* "Structure and Functioning of Estuarine Ecosystems Exposed to Treated Sewage Wastes" (E. J. Kuenzler and A. F. Chestnut, eds.), Annu. Rep. for 1970–1971, Sea Grant No. GH 103, Proj. UNC-10, pp. 205–238, University of North Carolina, Chapel Hill.

Ward, D. V., and Howes, B. L. (1974). The effects of Abate, an organophosphorous insecticide on marsh fiddler crab populations. *Bull. Environ. Contam. Toxicol.* **12,** 694–697.

Ward, D. V., Howes, B. L., and Ludwig, D. F. (1976). Interactive effects of predation pressure and insecticide (Temefos) toxicity on populations of the marsh fiddler crab *Uca pugnax*. *Mar. Biol.* **35,** 119–126.

Waterman, T. H., ed. (1960). "The Physiology of Crustacea," Vol. 1. Academic Press, New York.

Waterman, T. H., ed. (1961). "The Physiology of Crustacea," Vol. 2. Academic Press, New York.

Webb, D. A. (1940). Ionic regulation in *Carcinus maenas*. *Proc. R. Soc. London, Ser. B* **129,** 107–136.

Weis, J. S., and Mantel, L. H. (1976). DDT as an accelerator of limb regeneration and molting in fiddler crabs. *Estuarine Coastal Mar. Sci.* **4,** 461–466.

Welch, W. R. (1968). Changes in abundance of the green crab, *Cacinus maenas* (L.), in relation to recent temperature changes. *Fish. Bull.* **67,** 337–345.

Williams, A. B. (1965). Marine decapod crustaceans of the Carolinas. *Fish. Bull.* **65,** 1–298.

Williams, A. B. (1971). A ten-year study of meroplankton in North Carolina estuaries: Annual occurrence of some brachyuran developmental stages. *Chesapeake Sci.* **12,** 53–61.

Williams, A. B. (1974). The swimming crabs of the genus *Callinectes* (Decapoda: Portunidae). *Fish. Bull.* **72,** 685–798.

Williams, A. B., and Deubler, E. E., Jr. (1968). Studies on macroplanktonic crustaceans and ichthyoplankton of the Pamlico Sound complex. *N. C., Dep. Conserv. Dev., Div. Commer. Sports Fish., Spec. Sci. Rep.* No. 13, pp. 1–103.

Williams, B. G. (1968). Laboratory rearing of the larval stages of *Carcinus maenas* (L.) (Crustacea: Decapoda). *J. Nat. Hist.* **2,** 121–126.

Winget, R. R., Maurer, D., and Seymour, H. (1974). Occurrence, size composition and sex ratio of the rock crab, *Cancer irroratus* Say and the spider crab, *Libinia emarginata* Leach in Delaware Bay. *J. Nat. Hist.* **8,** 199–205.

Yang, W. T. (1971). Preliminary report on the culture of the stone crab. *In* "Proceedings of the Second Annual Workshop, World Mariculture Society," pp. 53–54. Div. Continuing Educ., Louisiana State Univ., Baton Rouge.

Young, J. E. (1974). Variations in the timing of spermatogenesis in *Uca pugnax* (Smith) and possible effectors (Decapoda, Brachyura, Ocypodidae). *Crustaceana (Leiden)* **27,** 68–72.

62